THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 50, No. 2, pp. 39-126 July 27, 1973

A Field Study of Costa Rican Lizards

Henry S. Fitch

TABLE OF CONTENTS

A Field Study of Costa Rican Lizards

Henry S. Fitch[1]

ABSTRACT

From October 1967 to March 1970 local populations of 26 species of lizards including gekkonids, iguanids, anguids, teiids, and scincids, were studied at 15 localities on 23 study areas in Costa Rica. Capture-mark-recapture procedures were used and the field records were supplemented by examinations of museum specimens. More than 17,000 field records were accumulated, representing tropical and subtropical rain forest, xeric lowland forest, gallery forest along streams, ocean beach, and various transitional situations. The species studied were a spectrum of ecological types; some were euryecic and showed significant ecological change from one study area to another with different habitat or climate. Preferred body temperatures ranged from 19.5°C in *Anolis tropidolepis* to approximately 40°C in *Cnemidophorus deppii*. Heliothermic species were found to have the highest body temperatures, *Ctenosaura similis* and *Ameiva undulata* maintaining levels only a little below that of *Cnemidophorus deppii*, and a little higher than the species of *Sceloporus*. In basilisks, skinks and most kinds of anoles, preferred body temperatures were found to be between 27 and 35.5°C.

Growth to breeding maturity occurred in 4 to 8 months in most kinds of small lizards, but the largest kinds required a longer time—at least a year in *Basiliscus basiliscus* and 2 years or more in *Ctenosaura* and *Iguana*. In most species marked individuals that were recaptured after intervals of a month or more had moved no more than 15 m, and typical home ranges of most species were judged to have radii in the range of 5 to 12 m. Reproductive cycles were found to be closely correlated with climate. In northwestern Costa Rica where there is little precipitation from December to April, most species including *Anolis cupreus, A. sericeus, A. intermedius, Ctenosaura similis, Ameiva undulata, Sceloporus variabilis* and *Cnemidophorus deppii* cease to produce eggs in the dry season. In the warm, humid climate of the Caribbean lowlands there is year-round reproduction in most species but its level changes throughout the annual cycle, with more egg-laying in the wetter months and less in the drier months. In *Basiliscus vittatus* and *Scincella cherriei* changes in the level of reproduction are most prominent; in *Anolis humilis* at San Miguel de Sarapiquí and *Gonatodes albogularis* at Limón there is relatively little change in the level of reproduction throughout the year. Most nearly uniform year-round reproduction occurs in *Anolis tropidolepis* in montane cloud forest in a climate that is cool and moist throughout the year.

INTRODUCTION

The present study was conceived in 1964, as an intensive and protracted investigation on a series of tropical reptile populations, with attention focused on reproductive cycles and the roles of various climatic factors in controlling them. Preliminary field work was done at many of the study areas in early 1965, but the main field effort was made during a continuous eight-month period in 1967-1968 with four shorter sojourns of one to two months each in late 1968 and 1969, and early 1970.

At the time of the study's inception relatively little had been published regarding the reproductive cycles of tropical reptiles but in the ensuing eight-year period much interest in the subject has developed, and many investigations have been under-

[1] Division of Biological Sciences, University of Kansas, Lawrence, Kansas 66044.

taken, some on the same species and even at the same localities involved in my own field work. These studies have generally concentrated on single species, often at a single locality. Much information is now available regarding the reproductive cycles of tropical reptiles, and some of the kinds herein discussed have already been studied. However, the present study was of longer duration than most, and comparative data were gathered for many species simultaneously. For some euryecic species, studied at two or more localities under different climatic conditions, there was especially favorable opportunity to assess the significance of temperature and moisture in the timing of events associated with reproduction. Although determining the effects of climatic factors on reproductive cycles was the prime objective, other interrelated aspects of the ecology were included in the study. Population structure was considered a key to understanding reproductive cycles, and population dynamics were investigated in each common species. Study of growth, by capture, marking, and recapture, constituted a major part of the total effort, as it was considered essential to an understanding of the annual cycle in each species.

Any kind of lizard that could be found in adequate numbers at a reasonably accessible locality was studied, but effort was made to include types representing diverse sizes, trophic levels, habitats, climates and phylogenetic groupings. The study was field oriented, and undertook to analyze natural populations without altering them. Procedure ordinarily did not involve removal of individuals, which were only momentarily restrained at the time of capture. The need for information regarding state of the gonads necessitated sacrifice of some animals, but their numbers were relatively small; ordinarily they were taken outside (but adjacent to) the areas that contained marked populations.

ACKNOWLEDGMENTS

Special thanks are due to my collaborators who without any material reward volunteered their services, accompanied me in the field, and labored long and arduously. These include Drs. Robert R. Fleet and Anthony A. Echelle, Alice Fitch Echelle, David C. Fitch, Chester W. Fitch and Virginia R. Fitch. At many of the study areas, local Costa Ricans graciously accompanied us in the field and aided us in the capture of lizards. Drs. Daniel H. Janzen and William E. Duellman kindly advised me in my choice of study areas. Dr. Duellman and his associates, Joseph T. Collins, Stephen R. Edwards and Dr. John Lynch also helped me by making identifications of the lizards studied, and by making available for my use the University of Kansas Museum of Natural History collections. Dr. Norman J. Scott and Jorge Campabadal of the Organization for Tropical Studies and Drs. Rafael L. Rodriguez and Douglas Robinson of the University of Costa Rica helped me in various ways. Amañ Rosales of the Costa Rican Servicio Meteorológico Nacional kindly permitted me to use unpublished weather data. Dan Sargent of Limón and Beverly extended many courtesies in permitting and encouraging my field work on his farm. The National Science Foundation provided financial support for my research with grant GB-6724.

METHODS AND MATERIALS

For sampling, 15 localities were selected distributed across Costa Rica from east to west and from north to south (Fig. 1). At some of the localities there were two or more study areas, depending on the local distribution and abundance of the species studied. Sampling ordinarily consisted of capturing the common species alive in large numbers, and processing each individual by measuring it, determining its sex and breeding status, and marking it for future recognition. Measurements were taken by pressing the animal against a ruler and reading to the nearest millimeter the snout-vent length, and tail

Fig. 1. Map of Costa Rica showing the 15 localities where population studies of lizards were made.

length with the original and regenerated parts recorded separately. Weights were recorded during the latter part of the study only, and were measured to the nearest tenth of a gram with Oskar Ludi spring scales. Reproductive condition of females was judged from their external appearance —whether collapsed and wrinkled from recent egg-laying, or of normal nongravid conformation, or slightly, moderately, or greatly distended with eggs or embryos. In some of the larger species, manual palpation confirmed the presence of unlaid eggs and provided information about the size and number of eggs in the clutch.

Lizards were marked chiefly by cutting off toes at approximately midlength. At least two toes were clipped on each lizard, always on different feet. In species that were processed in large numbers it became necessary to clip toes on three and eventually all four feet. Toe-clipping involved temporary laming and some permanent handicapping, especially in the scansorial and cursorial species, but alternatives such as branding, banding or tagging were judged to be even less satisfactory. Normally each lizard, besides being toe-clipped, was marked with a dab of paint before release. The color and position of

the mark occasionally served for individual recognition, but more frequently served to distinguish the recently processed lizards from others in the population.

In some of the populations studied, the lizards were so wary that capturing enough of them for an adequate sample would have consumed an inordinate amount of time. Also it would have resulted in bias, because the smaller and younger individuals are in some instances more readily caught than the larger and older. As a compromise lengths were estimated to the nearest millimeter in those seen at close range. Frequent checks, when the same individual was first estimated and then actually measured, showed that the percentage of error in the estimates was small after the observer had acquired sufficient experience.

Techniques for capturing lizards uninjured varied greatly according to the species and the situation. Anoles were usually caught by hand either on the ground or on vegetation. Effectiveness of stalking and securing the quarry with a rapid grab was tremendously increased by the discovery that the lizard could be "frozen" in position by presenting it with a "snakelike" object. A straight, smooth, tapered stick about five feet long was cautiously extended until a section of it was a few centimeters in front of the anole, then it was drawn slowly back and forth in a horizontal plane. Ordinarily this caused the anole to shift his attention from the person to the stick, and to respond with a characteristic crouching reaction. Then, continuing to move the stick, the operator could maneuver into position for the catch without causing the lizard to move. The ruse was most effective when two workers collaborated.

Another method that was highly effective for terrestrial species (*Cnemidophorus deppii, Sceloporus variabilis, S. squamosus, Ctenosaura similis* juveniles) in open, level terrain such as a sandy beach, involved coordinated teamwork of two to five collaborators using strips of sheet aluminum 0.4 m wide and 1.5 m long. When a lizard was discovered, the workers would surround it, attempting to head it off from dense cover where it might escape, and to maneuver it into an open place. Then they slowly converged, with metal strips bowed and held on edge near ground level. At a signal all simultaneously lowered and advanced their strips, so that the ends overlapped and the strips formed a continuous barrier corralling the quarry. Sometimes the capture was made only after a long and strenuous chase, but under favorable circumstances as many as ten captures with two or three species were scored simultaneously as the lizards were driven along a hedge or other natural travelway into the open corral and the entrance closed at the right moment.

Lizards climbing on tree trunks and fence posts often were caught by hand. The stalker approached unseen from the side away from the lizard, after noting its position. Effectiveness of capture was increased if a second person in the vicinity kept the lizard under observation, diverted its attention, and directed movements of the stalker, especially the final grab.

Noosing was the best method of capturing some kinds of shy, fast-moving lizards. Copper wire nooses on the ends of tapered sticks or poles about 2 m long were used. Skinks (*Scincella* and *Mabuya*) and geckos (*Gonatodes*) were caught by hand.

Relatively small numbers of lizards were collected and preserved to serve as voucher specimens, and for internal examination, mainly investigation of the gonads. Testes were measured in males. Most of the specimens collected were females, and they were examined for presence of yolked follicles and uterine eggs or embryos, which were measured, and for

corpora lutea. The University of Kansas Museum of Natural History contains much Costa Rican and nearby material, some of which is of the same species that I studied, and even from the same or nearby localities. These specimens supplemented my own collections.

Study areas were sampled in a sequence which varied from time to time, and an average interval of approximately six weeks elapsed between successive samples. Because of the large number of areas involved, and the amount of time spent travelling, an average of only a little more than two days was available for each sampling.

I visited many of the study areas for the first time and made preliminary observations and collections in February and March 1965. The field studies were carried out 13 Oct. 1967 to 17 July 1968, 8 Aug. to 8 Sept. 1968, 18 Jan. to 13 March 1969, 8 Aug. to 8 Sept. 1969, and 29 Jan. to 14 March 1970.

CLIMATIC FACTORS

The broad spectrum of climates within the radius of 154 km encompassed by the study areas obviously controlled distribution, abundance and behavior of the species studied. The proximity of two oceans, and lofty mountain ranges differing in their directional trends, often produce striking climatic change within a relatively short distance. All localities were latitudinally well within the Tropical Zone, from Quepos 9° 26′ N on the south to Playas del Coco 10° 34′ on the north, and from Playas del Coco 85° 44′ on the west to Limón 83° 03′ on the east.

The Cordillera de Guanacaste, C. de Tilarán, C. Central and C. de Talamanca form a nearly continuous chain through Costa Rica from northwest to southeast, separating the hot and humid lowlands to the north and east on the Caribbean Coast from the sometimes dry lowlands of the Pacific slope. Scott (1966) emphasized the important effect of dependable northeasterly trade winds on the Caribbean versant, and the influence of seasonal winds on the Pacific versant. In this classification the study areas fall into five climatic zones, as follows:

Wet Atlantic Lowland (Portéte, Limón, Beverly; less typically, San Miguel de Sarapiquí, Turrialba and Cartago) is characterized by high rainfall relatively evenly distributed throughout the year. According to Scott, rain is almost equally probable at any time of the day or night. The cloud cover is persistent, effectively and significantly cutting down insolation, evaporation and temperatures. Average relative humidity is high, and evaporation rarely exceeds precipitation over any lengthy period. Temperatures are moderate, with relatively large daily fluctuation but little seasonal change. Scott (1966) stated ". . . Insect populations maintain themselves at a fairly constant level throughout the year." Figures 2, 3A and 4 summarize weather records for this zone.

Wet Pacific Lowland (Quepos) is characterized by high rainfall, but a marked dry season, with relatively little rain from December through April. Rain falls chiefly in the afternoon and evening. Temperature tends to be high and relatively uniform. Figures 3B and 5 summarize weather records for the Quepos area.

Dry Pacific Lowland (Playas del Coco, Sardinal, Finca Taboga, La Irma, Boca de Barranca) is characterized by high average temperature and low rainfall (especially during the dry season, December through most of April). Even during the rainy season, mornings are often cloudless, permitting a high evaporation rate, and almost all rain falls during the afternoon and night. Evaporation rate is high throughout the year, and exceeds precipitation for about eight months. There are strong north winds early in the dry season,

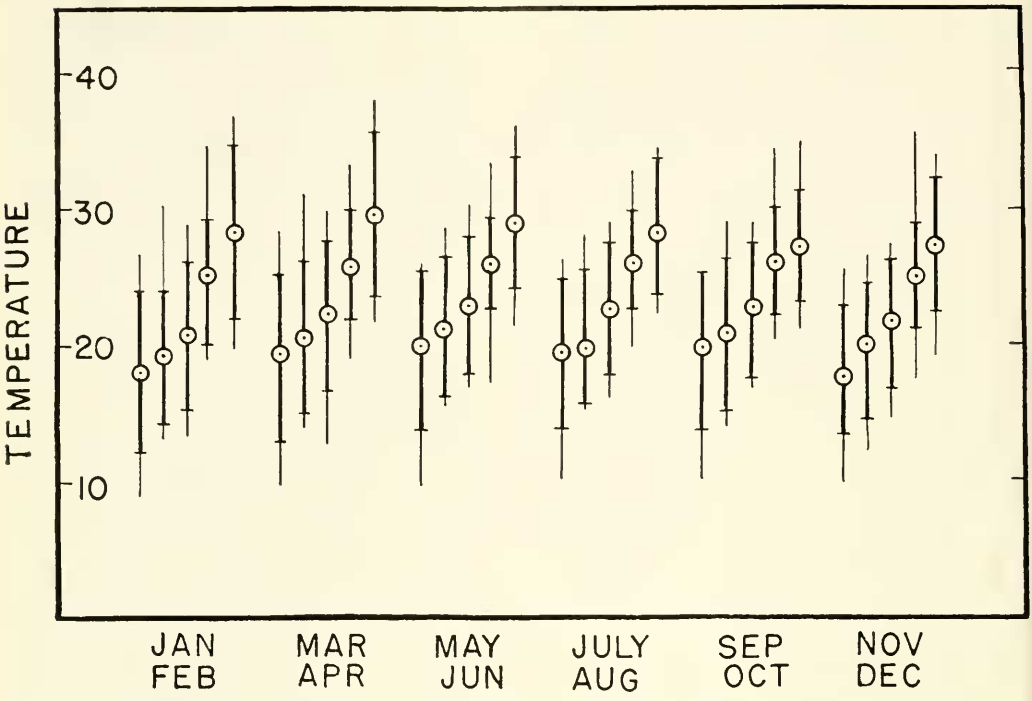

FIG. 2. Annual temperature range shown in bimonthly intervals for five sites representing six localities. From left to right in each group, vertical bars represent Cartago, San José, Turrialba, Limón, and Filadelfia (near Playas del Coco and Sardinal). For each site and bimonthly period, mean, mean minimum, mean maximum and extremes are shown (from Anuario Meteorológico, 1966, 1967, 1968, Servicio Meteorológico Nacional, Costa Rica).

December through February. For the remainder of the year winds are relatively mild and often are westerlies. (See Figs. 2, 3B and 5.)

Dry Pacific Intermediate (San José, Las Pavas) is characterized by a rainfall pattern similar to that of the Dry Pacific Lowlands but lower temperatures. The lower temperatures retard evaporation, and relative humidity remains fairly high, hence the dry season is less severe than in the lowlands. (See Figs. 2, 3B and 6.)

Wet Atlantic Intermediate (Hacienda El Prado) is characterized by high rainfall and cool temperatures the year around. Evaporation is generally low, but exceeds precipitation in February and March. High winds are frequent. (See Figs. 3B and 6.)

Statements in the foregoing paragraphs are generalizations which apply more or less to the specific study areas, but each area has its own climatic pecularities and some deviate markedly in unexpected ways from the mode of the broad zones in which they have been included. No field records of weather were kept in the course of my study, but instead records of the Servicio Meteorológico Nacional of Costa Rica were utilized. In the published annual reports of this agency data from many field stations are included, but the field stations contributing and the kinds of information provided by them differ from year to year. Also, in most instances the field stations are somewhat removed from the actual study areas and hence provide only approximations of their climatic traits.

Figures 2 to 6, based on records of the Servicio Meteorológico Nacional (1966, 1967, 1968), show climatic characteristics

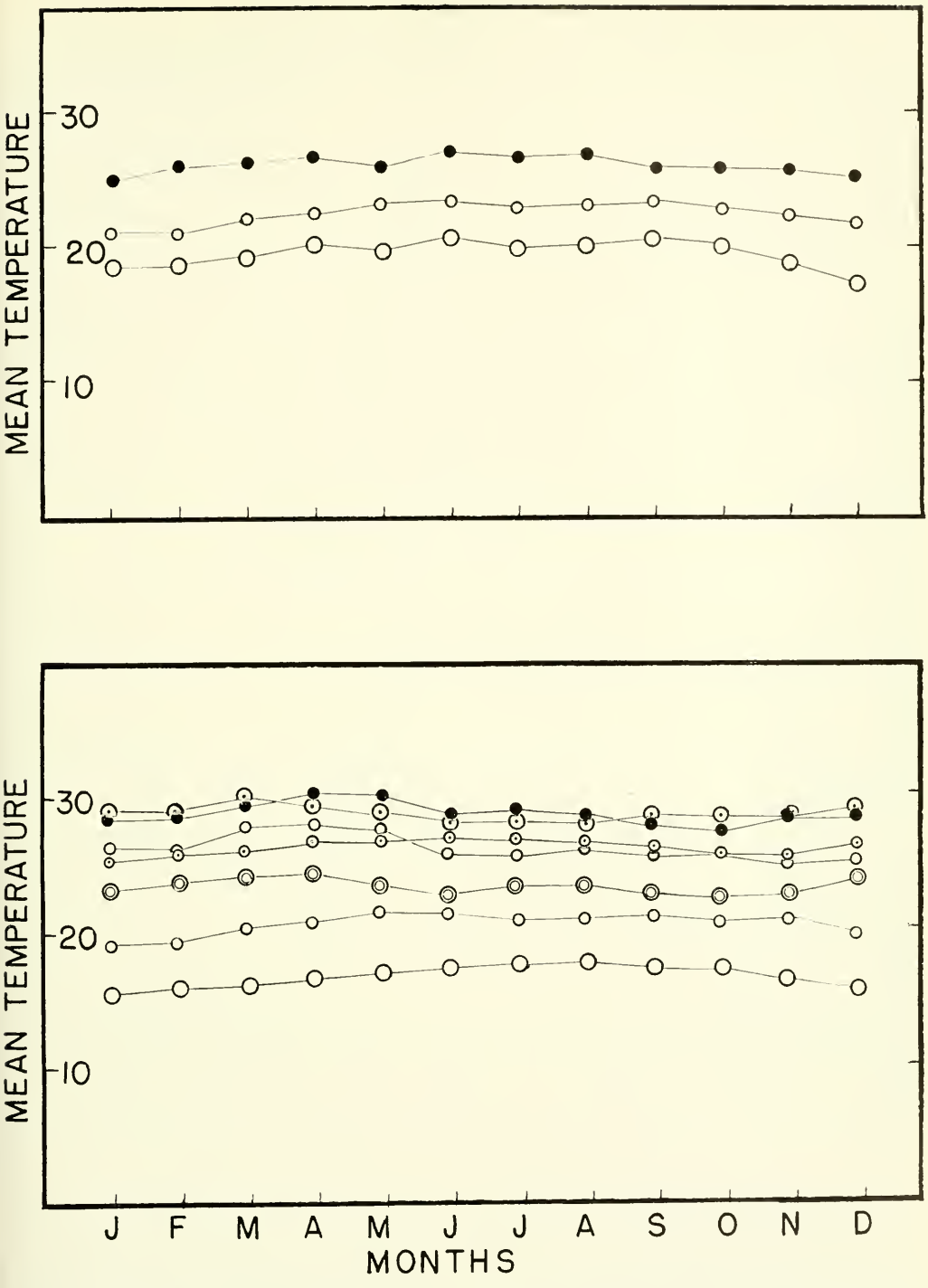

FIG. 3. A (above). Mean monthly temperatures at three localities of the Caribbean versant: solid circles, Limón; small open circles, Turrialba; large open circles, Cartago. B (below). Mean monthly temperatures at seven sites representing eight localities of the Pacific versant: small solid circles, Filadelfia (near Playas del Coco and Sardinal); large circles with dots, Puntarenas (near Boca de Barranca); small open circles (of upper series), Las Juntas (near La Irma); small circle with dot, Parrita (near Quepos); double circles, Santa Ana (near Las Pavas); small open circles (of lower series), San José; large open circles, Vara Blanca (near Hacienda El Prado). (Same source as Fig. 2.)

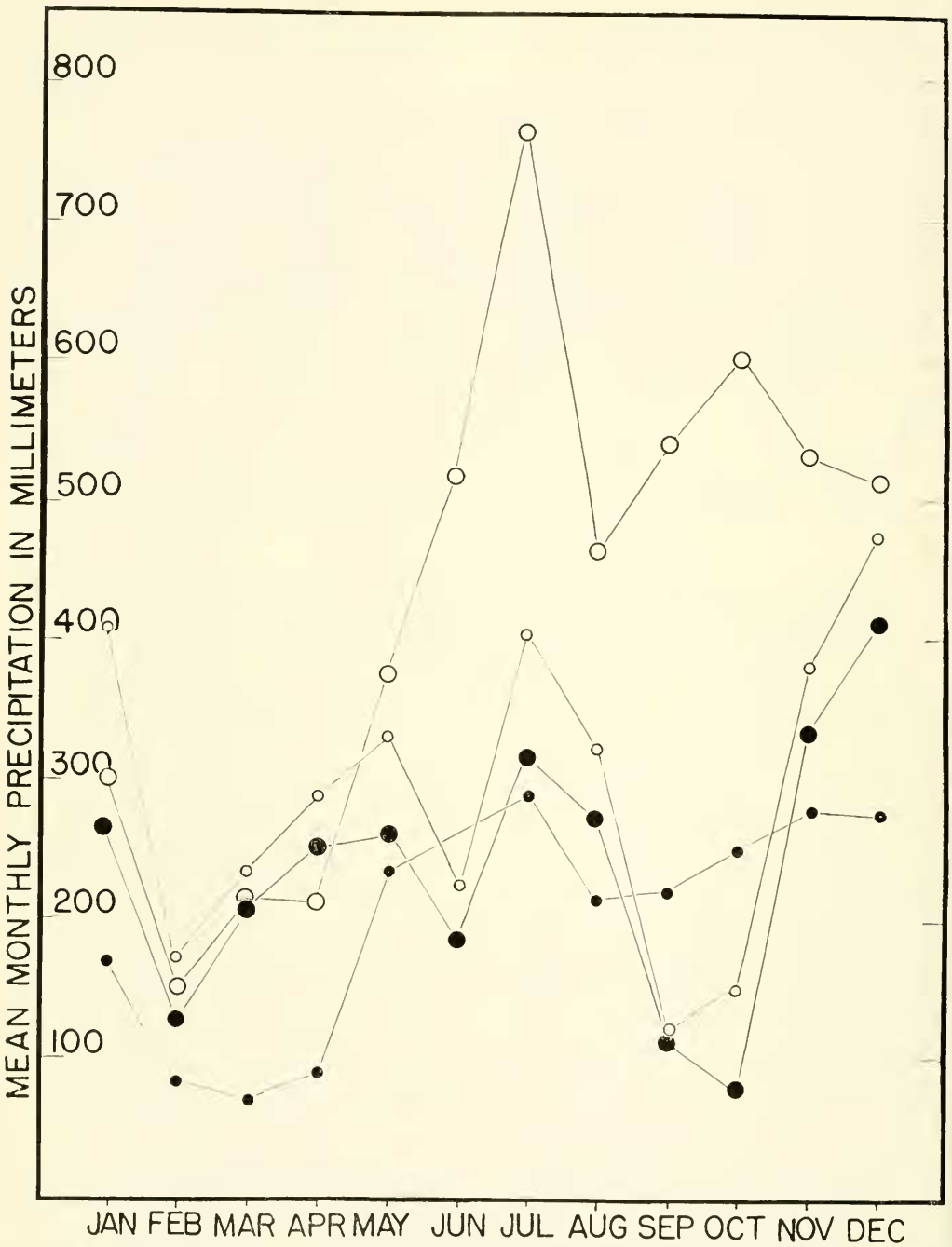

FIG. 4. Mean monthly precipitation at four localities of the Caribbean versant: large open circles, San Miguel de Sarapiquí; small open circles, Limón; large solid circles, Beverly; small solid circles, Turrialba. Records for San Miguel are five-year averages (1961-1965); others are ten-year averages (1956-1965). (Same source as Fig. 2.)

of weather stations near the study areas. The study area at Hacienda El Prado near Vara Blanca was at the Continental Divide, but was actually in the Pacific drainage. However, Vara Blanca has a climate more characteristic of the Atlantic versant

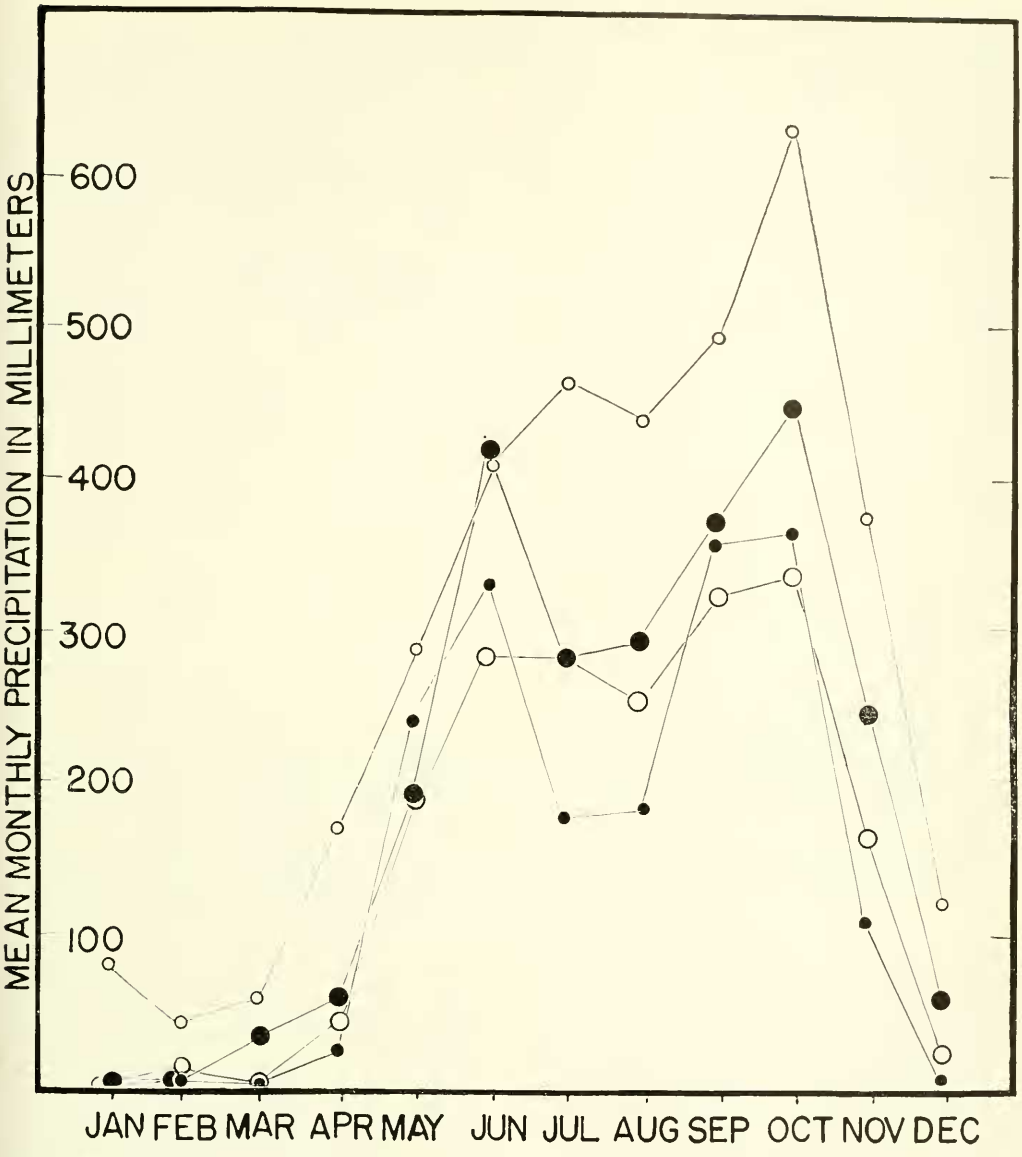

Fig. 5. Mean monthly precipitation at four sites representing five localities of the Pacific versant: small open circles, Quepos; large solid circles, Las Juntas (near La Irma); large open circles, Boca de Barranca; small solid circles, Filadelfia (near Playas del Coco and Sardinal). Records for Las Juntas are averages for years 1961 to 1965; others are averages for years 1956 to 1965. (Same source as Fig. 2.)

—high precipitation for the most of the year, including December and January. The study area represented by San Miguel de Sarapiquí is about 4 km south of the town and farther in the mountains, where climate is somewhat cooler and wetter. Cartago, situated on the Caribbean versant at medium-high altitude, could be expected to have a cool and moist climate, but the records indicate that it is remarkably dry. Annual precipitation (1961-1965) averaged only 1107.3 mm, much less than at any other station in Costa Rica. Presumably low precipitation is correlated with the presence of Volcán Irazú (3432 m) 16 km north-northeast intercepting

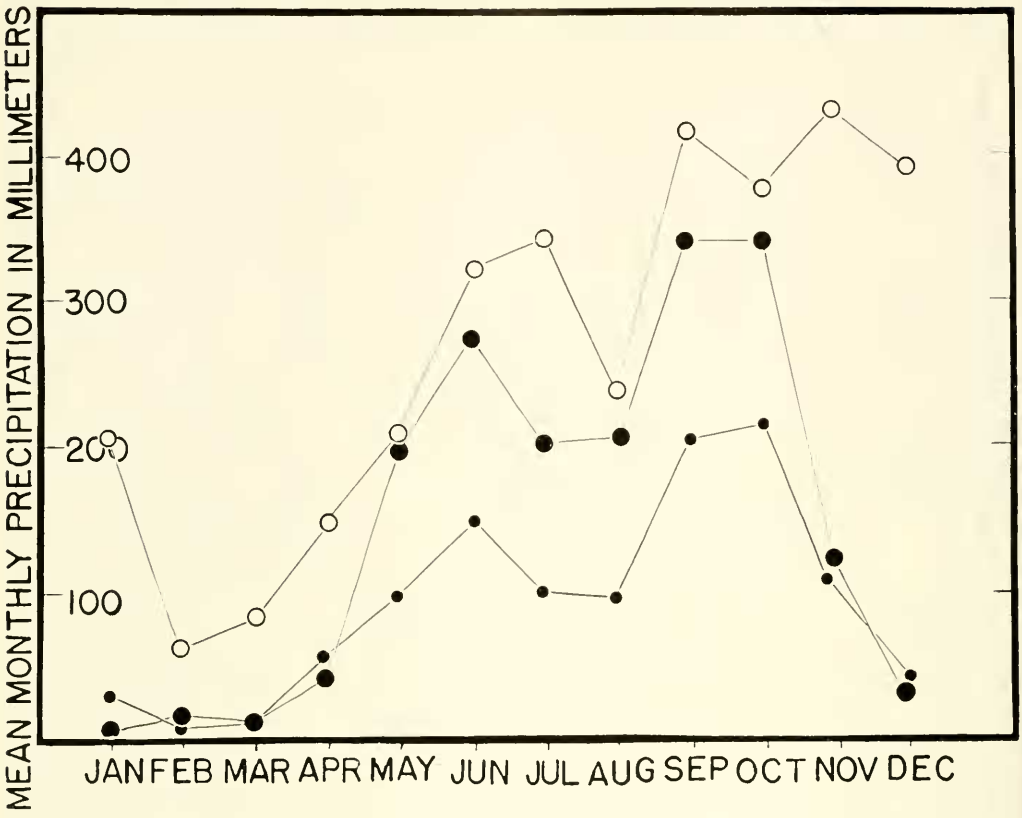

FIG. 6. Mean monthly precipitation at three sites representing localities of the Meseta Central; large open circles, Vara Blanca (near Hacienda El Prado); large solid circles, San José; small solid circles, Cartago. Records for San José are averages for years 1956 to 1965; those for Cartago and Vara Blanca are averages for 1961 to 1965. (Same source as Fig. 2.)

moisture-laden air from the Caribbean and casting a rain shadow. Turrialba, situated nearer the Caribbean Coast and at lower altitude than Cartago, has a much wetter climate, but here too the weather records show less precipitation than might be expected, and the mountain mass of Volcán Turrialba (3328 m) 16 km approximately northwest probably affects local rainfall to some extent. Portéte on the Caribbean Coast just west of Limón, and Beverly 12 km south on the coastal plain show almost identical trends in annual precipitation, but with consistently greater amounts each month at Portéte. There are definite peaks in May, July and December, with relatively meager precipitation in February, June and September-October. San Miguel de Sarapiquí, situated on the lower slopes of Volcán Poas on its Caribbean side, has one of the wettest climates in the country, but rainfall is subject to marked seasonal change, with a peak in July and relatively meager precipitation in February, March and April. Playas del Coco and Sardinal are believed to be adequately represented by the records kept at Filadelfia 20 km and 14 km SE, respectively, but Filadelfia is somewhat more removed from the moderating influence of the ocean. The study area at La Irma, Río Congo, is represented by the station at Las Juntas approximately 4 km distant, but Las Juntas is 100 m higher and probably has a somewhat cooler and wetter climate. In the Pacific lowlands (Filadelfia, Las Juntas, Boca de

Barranca) the peak of the rainy season is in October and dry season extends from December through April. A characteristic feature is the *veranillo,* a minor dry season in July and August which separates the peak precipitation of October from a lesser peak in June. The *veranillo* is scarcely noticeable in the records from Quepos, which has a much wetter climate than the other localities of the Pacific lowlands. Quepos is allocated in the Pacific Wet Lowlands, but has much less precipitation than lowlands of extreme southeastern Costa Rica; actually it is in a zone that is transitional between this area and the Pacific Dry Lowlands of northwestern Costa Rica.

STUDY AREAS

Field work was conducted on 23 separate study areas (not all used concurrently) at the 15 localities shown in Figure 1. Kinds of lizards present and the numbers of them recorded at each locality are shown in Table 1. Areas differed greatly in size and shape, and in stability of their lizard populations. The areas were originally chosen on the basis of having high populations of lizards, of being relatively accessible, and of representing distinct types of habitat and climate. During my field work most of the original study areas were grossly disturbed—by flood and high tide in some instances, but usually by human activities such as tree-cutting and bulldozing, resulting from rapidly expanding population and industry. Such occurrences seriously hindered my studies and necessitated change in the routine of sampling and, sometimes, transfer of operations to other areas. Areas utilized were the following:

Playas del Coco, Guanacaste Province, 1-3 m. Two study areas selected were similar fenced seaside lots (without buildings) in a resort subdivision. Area no. 1 was 107 m x 32 m but its southeastern part, 55 m x 10 m, was a dense thorny thicket, which was excluded. A lane 8 m wide on the south edge of the original study area, and the fence bounding an adjacent lot, were incorporated after the first sampling. The area extended inland from the crest of the beach dune. Near the crest were low patches of sea grape *(Coccoloba uvifera).* A hedge of cactus-like euphorbiaceous plants 2 to 3 m high bounded the lot on its ocean front to the west and on the south side and part of the north side. The part nearest the ocean was a sand field with three large tamarinds *(Tamarindus indica)* and with open areas of low weeds, and bare ground riddled with the burrows of land crabs. The field sloped to a bare swale which sometimes held water in the rainy season. Beyond the swale the lot was wooded. There were six coconut palms *(Cocos nucifera)*; a tree of *Cassia grandis* nearly 1 m in trunk diameter dominated the eastern part, and there were smaller trees of *Delonix regia, Terminalia catappa* and *Spondias* sp. Early seral herbs, and shrubs such as ant plants *(Acacia cornigera)* were abundant.

Cnemidophorus deppii was abundant, especially on the more open and sandy part, and at the front hedge. *Sceloporus variabilis* was common on and near the larger trees and some lived in the hedge or on fence posts. *Ctenosaura similis* tended to keep near the larger trees or the denser parts of the hedge. *Ameiva undulata* stayed in or near the thicket in the northeast part of the lot. *Anolis cupreus* was occasionally found on stems of shrubs or low on the trunks of the smaller trees. Several *Sceloporus squamosus* were found in the lane bordering the lot and in adjacent barren fields. *Anolis sericeus* was rare; the few individuals found were on fence posts in more open situations than those frequented by *A. cupreus.*

Ctenosaurs were occasionally hunted

on the area by persons armed with small bore rifles or by children with dogs. Otherwise there was little direct effect on the lizard populations by humans. Many vehicles and pedestrians moving up and down the beach passed along the front hedge. At intervals of several weeks, crews of *macheteros* cleared brushy and thorny low vegetation, which was stacked and burned, probably eliminating some lizards that had resorted to the piles for shelter. Horses, hogs, dogs, and chickens ranged over the area. Wildlife was not abundant; potential predators on lizards that were noted were the armadillo *(Dasypus novemcinctus),* the Magpie Jay *(Calocitta formosa)* and a snake *(Conophis lineatus).*

Area no. 2 was 35 m x 31 m and was chosen for study of *Sceloporus variabilis,* but most species noted on no. 1 were present here also. This lot was 1 km farther north than no. 1, near the end of the beach, and there was little human activity. The study area was the front (west) half of a lot dominated by two *Bombacopsis quinata* trees 2 m and 1.3 m in trunk diameters (Plate 1, lower). Seven trees of *Delonix regia* averaging 0.2 m in trunk diameters were distributed over the area. Other small trees or shrubs included *Coccoloba* sp. and *Terminalia catappa.* Weedy shrubs, especially ant plants, were abundant. Clumps of low vegetation provided effective refuge for the lizards.

Gonatodes albogularis was not seen on either study area, but was abundant on several large strangler fig trees (*Ficus* sp.) and occasionally on smaller trees, fence posts, walls and rocks along the southern part of the beach where human activities were most concentrated.

Sardinal, Guanacaste Province, 90 m. The study area was approximately 0.5 km northwest of the village, and extended 100 m up a ravine from its outlet into the Río Sardinal. The ravine ran parallel to a road on its south side. Cultivated fields were on both sides, and nearby slopes were heavily grazed, with vegetation of xeric aspect, but the ravine and its vicinity were more mesic, with a remnant forest including giant trees of *Terminalia* and other kinds forming a band about 50 m wide. The ravine had steep banks, usually 3 m or more high. In the dry season there was little more than a seepage in the ravine bottom, and even in the rainy season there was usually only a small volume of water flowing. Leaf litter carpeted the ground and accumulated in thick masses along the ravine bottom, but bare soil was exposed along the steep banks. Dense brush and luxuriant herbaceous vegetation grew in some places, but was periodically trimmed at the edges of the fields by *macheteros.* Barbwire fence separated the grove from adjacent fields. Humans were rarely seen on the study area, but many passed on the road either on foot or on horseback. Hogs and occasional horses and cows were on the study area. The Roadside Hawk *(Buteo magnirostris)* was occasionally seen and frequently heard in the grove. *Anolis cupreus* was extremely abundant in and along the ravine and was the main species studied. *Ameiva undulata* was common in the grove and along the edges. *Ctenosaura similis* was moderately common. *Gonatodes albogularis* was often seen on bases of the large trees and on fence posts. *Basiliscus basiliscus* was occasionally seen in the ravine and was abundant along the river nearby. *Iguana iguana, Sceloporus variabilis, Sceloporus squamosus, Anolis sericeus,* and *Cnemidophorus deppii* were seen from time to time.

Finca Taboga, Río Higuerón, Guanacaste Province. The area was on the coastal plain near sea level. From a bridge across the river the study area extended in one direction approximately 1 km upstream where the diked and channelized stream flowed through cleared pastureland with tall rank grass. A second segment

extended through swampland forest from approximately 2 km to 4 km below the bridge. This lower reach of the river was much less altered and the channel followed a meandering course. Giant trees, guanacastes *(Enterolobium cyclocarpum)* and others, were numerous, but much of the vegetation was scrubby and thorny. Oxbows, marshes and ponds alternated with higher ground. Flooding was extensive in the rainy season. The river's course was frequently obstructed by log jams and large fallen trees. Banks were frequently undercut, with exposed tree roots or vine tangles. The river was often 5 to 10 m across and 0.5 to 2 m deep.

Basilisks were abundant along both stretches of the river, and were concentrated where shelter was most plentiful. Iguanas were numerous, especially in the swamp forest. Ctenosaurs were seen mostly in dry pasture land. Under favorable conditions many were seen from the road.

The Finca Taboga area was less densely populated by humans and was less subject to gross disturbance than most of the other areas studied. However, crews of laborers were regularly trucked to the area for work in cultivated fields, for machete clearing of pasture land or less frequently for fence building or road construction in the swamp. Here as elsewhere, ctenosaurs and iguanas were subject to some persecution, but their numbers were seemingly not much affected. Wildlife abounded in the area. Doubtless many kinds of mammalian predators were present, but predatory birds were much more in evidence. These included the Crested Caracara *(Polyborus cheriway)*, Laughing Falcon *(Herpetotheres cachinnans)*, Common Black Hawk *(Buteogallus anthracinus)*, Gray Hawk *(Buteo nitidus)*, Roadside Hawk, Broad-winged Hawk *(B. platypterus)*, Wood Stork *(Mycteria americanus)*, Common Egret *(Casmerodius albus)*, Great Blue Heron *(Ardea herodias)* and many others. Snakes observed included *Boa constrictor*, *Conophis lineatus* and *Crotalus durissus*.

La Irma, Río Congo, Guanacaste Province, 100 m. The study area was along the river approximately 1.5 km NNE of La Irma. Land was cattle range of rolling hills, with occasional large trees or patches of scrubby forest. A mesic gallery forest followed the stream intermittently with trees of *Terminalia* and others, some of giant size. Between gentle slopes the stream followed a meandering course in a narrow bottom with a gravel bed and occasional sand deposits. There were cutbanks, sometimes as much as 3 m high, bare or with exposed tree roots or sometimes mantled with vines and other luxuriant vegetation. In other places the terrain sloped gradually to the edge of the water. Series of shallow riffles alternated with deep pools. Many of the trees grew at the edge of the bank, with roots on one side exposed or undermined. Flow was highly variable. In the rainy season the river often overflowed its banks and cut new channels, whereas in the dry season the flow between pools was reduced to a trickle. In times of flood massive deposits of drift accumulated in log jams (Plate II, lower) and on the banks. On most of my visits the flow between pools was 0.1-2 m deep and 1-5 m wide.

At this locality, greatest effort was devoted to a study of *Basiliscus basiliscus;* it was hunted along the stream for a linear distance of approximately 0.5 km, but because of the winding course of the stream, the opposite ends of the study area were only about 150 m apart. *Anolis cupreus* was found in phenomenal abundance in a strip within a loop of the creek on its left bank, an area approximately 50 m long and 15 m wide. In June 1968, after heavy flooding, however, lizard populations were much reduced.

The entire area was heavily grazed and trampled by cattle, but there was little human activity. Horsemen occasionally rode across it and on several occasions hunters with firearms were seen stalking iguanas. Wildlife was abundant. Howler monkeys *(Alouatta palliata)* were seen or heard many times daily. Predators that might have affected lizard populations were numerous and included hawks *(Buteo magnirostris),* and herons *(Ardea herodias, Casmerodius albus).*

Boca de Barranca, Puntarenas Province, 1-3 m. Two separate study areas, each with several parts, were used. The first area centered on the grounds of the Marbella Hotel, a beach resort on the north side of the Río Barranca at its mouth. The hotel buildings were situated on the front dune only a little above high tide mark. They included a large pavilion, dormitories, and various accessory small buildings. The hotel grounds extended 220 m along the beach and 140 m back from the crest of the dune. Numerous coconut palms and other trees both native and exotic were scattered over the grounds (Plate II, middle). There were two giant tamarind trees, flower beds, weedy and grassy areas, lines of boulders along the entrance driveway for 150 m, piles of trash mainly of coconut fronds that were periodically burned, and other more permanent trash heaps of scrap metal, broken glass and a variety of wooden and plastic articles. The sand beach on the ocean side of the hotel grounds varied in extent and conformation, being frequently altered by high tides and storm. Sea grapes and tall coarse grass stabilized parts of the dunes and provided some shelter. Beach wrack consisting of logs, boards and sticks with an intermixture of discarded articles was especially abundant near the river mouth. At high water mark, masses of wrack accumulated, interwoven and anchored by logs and palm fronds partly buried in the sand, and providing an abundance of hiding places for lizards and other small animals. North of the hotel grounds a series of private resort homes, each on a lot several acres in extent, faced onto the beach. Some of the lots were enclosed by fences. Some had groves of ornamental or fruit trees. *Sceloporus variabilis* was studied not only on the hotel grounds but along the line of beach wrack (Plate II, upper) for nearly 1 km to the north. *Ctenosaura similis, Cnemidophorus deppii,* and *Gonatodes albogularis* were studied mainly on the hotel grounds, where all of them were abundant.

On weekends and especially during the holiday season of February and March, vacationers, greatly outnumbering the resident population, visited this resort. Occasionally boys with slingshots, air rifles or firearms killed lizards. Ctenosaurs especially were subjected to constant persecution, being considered pests because of their digging activities, and were also hunted for sport and for their edible flesh and unlaid eggs. Dogs, cats, hogs, chickens and turkeys ranged freely over the hotel grounds and all of them preyed upon lizards. Chickens and cats especially were believed to have reduced the numbers of some kinds of lizards and perhaps had eliminated *Anolis cupreus* which was not found on the hotel grounds.

The second area, on the south side of the river's mouth, was allotted relatively little time and *A. cupreus* was the only species studied there. A steep hill overlooked the river and there was a series of small inlets with narrow sandy or rocky beaches and steep banks or cliffs rising precipitously from the shoreline. A scrubby xeric forest with many kinds of native trees, shrubs and vines extended down to the ocean edge at the base of the bluff. The area was little altered by human activity. A few isolated shacks of fishermen and other residents were scattered along

the lower end of the river, and on holidays and weekends picnickers and hikers crossed the river in rented rowboats.

Quepos, Puntarenas Province, 0-70 m. Field work was concentrated in a beach area 3-4 km northwest of the town and just south of the mouth of the Río Cañas. Here there were extensive stretches of open sand, and quantities of wrack carried down by the river had accumulated at high tide level. Cordgrass formed a mat over the dunes in places. Groves of coconut palms grew on the crest of the dune and its lee side down to the edge of a mangrove swamp. Banana plantations occupied part of the dune. At the north end of the dune beyond the plantations an area of natural vegetation estimated as 2 hectares bordering the swamp had a dense thicket of cane and spiny palm. There was little human activity on the area but occasionally fishermen, bathers, and hikers crossed it, and charcoal burners sometimes worked there. Individuals or small groups occasionally came to hunt iguanas with guns and dogs. *Ameiva quadrilineata* was the main study species. These lizards were difficult to catch but easy to observe. During late spring and summer young ctenosaurs were abundant.

Hacienda El Prado, Alajuela Province, 1910 m. The study area of 2 hectares was approximately 5 km west of Vara Blanca and was bounded on the north by Costa Rica Highway 120, here following the Continental Divide in montane cloud forest on the southeast slope of Volcán Poas. The area was used as pasture and the original forest of *Oreopanax jalapensis, Drimys, Quercus, Trema, Turpinia, Eugenia, Sloanea, Bocconia, Spondias* and other trees had been largely destroyed, but there were scattered living trees, some of giant size. A spongy mat of dense grass, often 0.1 m thick, covered the ground, and logs, stumps and tree trunks similarly supported a luxuriant, spongy growth of epiphytes of many kinds.

Fenced pastures within the study area were alternately subjected to heavy grazing and then retired from use for periods of weeks. Workers periodically trimmed back sprouts and epiphytes, checking the spread of woody vegetation. On 21 Jan. 1969 clearing operations were in progress and most of the remaining large trees on the area were cut and burned, drastically reducing the numbers of lizards. The only potential predator noted on the area frequently was the Brown Jay *(Psilorhinus morio). Anolis tropidolepis* was the main species studied; *A. intermedius, Sceloporus malachiticus,* and *Gerrhonotus monticola* were found infrequently. Some of the records for all four species were obtained on a nearby area of similar habitat 1 km south of Vara Blanca (Heredia Province) in October and November 1967 and January 1968.

San Miguel de Sarapiquí, Alajuela Province, 500 m. This study area was on the northeast slope of Volcán Poas, beside Highway 9, between San Miguel and Cariblanco, and on a west branch of the Río Sarapiquí 100 m upstream from where the highway crosses the river. The lower half of the study area was essentially an island in this stream, but on the right side of the main channel. The upper part of the area was along the streambank. The stream was swift and clear in a rocky bed, with gravel and cobble along its edges and with many protruding boulders. The stream was usually 0.5 to 2 m deep, with steep banks, and a fairly stable flow of water. Rain forest vegetation covered the study area. There were large trees of many species, with buttressed roots; tree trunks and limbs were heavily laden with epiphytes, especially bromeliads. Moss and lichens grew in a thick carpet on tree trunks and rocks. Lianas were abundant. Ground was covered with a carpet of dead leaves and also supported a luxuriant growth of low herbaceous broad-leafed

vegetation except where high water had swept away vegetation and debris. Masses of drift and debris accumulated over obstructions. The study area was 150 m long and 10 to 50 m wide, bordered for part of its length by a long, narrow strip of bottomland pasture and for the remainder by precipitous slopes.

No humans were ever seen on the study area, and presumably it was so rarely visited that persons had little direct effect on its lizard populations. Access from the road was hindered by steep slopes with cliffs or by the swift and deep current of the stream. Horses and cattle occasionally ranged over the study area. No other domestic animals were known to visit it. Wildlife including predators was probably common, but animals were not readily seen or heard because of the dense cover and the roaring of the swift water.

San José, San José Province, 1197 m. Several study areas were used in the eastern part of the city, but they changed throughout the course of field work. Although lizards were abundant at certain times and places, the expanding human population and booming economy frequently caused their disturbance or destruction in the places chosen. One area extended along the right-of-way of the Northern Railway west southwest from Highway no. 202 (near the University of Costa Rica campus) about 1 km, to Calle 39. For most of this distance the railway was bordered by groves of coffee trees. Barbwire fences utilizing living trees (usually *Gliricidium*) as posts (Plate 1, upper) separated the railroad strip from private property adjoining. Tall grass grew in the ditches along the railroad bed and the fences. Occasionally machete crews cut the grass and trimmed the sprouts on the *Gliricidium* tree fence posts. Lizards were found chiefly on the fence posts, sometimes on trees, including the coffee trees and larger shade trees in the cafetals. *Anolis cupreus* was nearly always the most abundant, and was the main object of study. *A. intermedius* was usually less numerous, but it outnumbered *A. cupreus* along a line of yuccas fronting a coffee factory for 100 m. *Sceloporus malachiticus* was present in relatively small numbers.

A second major study area was 200 m south of the east end of the first in the large lot of the Eldorado Apartments. Many trees grew in the lot, which was bounded on the north by a fence and cafetal, and on the west by a concrete wall. In the northeast corner was an extensive pile of tree cuttings and trash. From time to time crews of workers cut the grass and trimmed the sprouts on the trees. By June 1968 lizards had become relatively scarce, both along the railroad and at the lot.

Population samples were subsequently obtained from several other areas as follows: 1) a lot at the corner of Avenida Central and Calle 29, about 50 x 50 m. *Anolis cupreus* was found on fence posts and walls around the edge. 2) A large vacant lot south across Avenida Central from the Eldorado Apartments. This lot had many large trees and had a remnant of a coffee grove along its east edge. It was especially productive of *A. intermedius* when first sampled in August 1968, but in March 1969 trees were cut and the lot was bulldozed, resulting in the virtual extermination of the lizards. 3) A small lot 200 m south of no. 2, in the Montes de Oca district. This lot was traversed by a ravine with a small stream, and high weeds and grass grew on it. Alice Fitch Echelle marked many *A. intermedius* and *A. cupreus* and made observations on their behavior from March through June 1968. 4) A lot at Avenida 12 and Calle 25 where population samples of *A. cupreus* were collected from time to time in 1968, 1969 and 1970. 5) A large lot on the north side of Avenida 10 and west side of Calle 27

first sampled in June 1968 and subsequently made the basis for marking operations in 1969 and 1970. Eventually it yielded more records than all the other areas combined. For much of its perimeter this lot was enclosed by cement walls, and tall coarse grass grew over most of it. *A. cupreus* and a few *S. malachiticus* were found chiefly on the lower parts of the walls and at their bases, and were found in trees, shrubs and grass tussocks, but relatively few were found in open areas.

All the study areas were surrounded by human dwellings and use of the areas by humans was heavy. Trampling and littering with discarded objects of many sorts affected the habitats. Also at times persons made active search for lizards to destroy them. Our own activities tended to draw attention to the lizards, and probably increased this sort of mortality. Cats, dogs and rats *(Rattus rattus)* were often seen on the study areas and may have preyed on the lizards occasionally. Of native animals that were potential predators, the Brown Jay was the only kind noted frequently. Insecticides, including chlorinated hydrocarbons, were being heavily used in San José at the time field work was in progress. Especially in the cafetals, heavy spraying may have caused direct poisoning of the lizards or may have affected them by ingestion of poisoned insects. Although success in hunting the lizards was much affected by the weather and recent cutting of thick vegetation, it is certain that the population on each area underwent drastic reduction at one time or another in the course of my work, and poisoning by insecticide seemed the most plausible explanation except in cases where the habitat was destroyed or grossly altered.

Las Pavas, San José Province, 1100 m. The study area was 2 km northeast of the village which is a suburb on the west side of San José. In an urbanization program an area of several hectares had been subdivided into city blocks, with paved streets, poles for street lights, and sewers, but with only a few occupied houses, and with grass and weeds over the lots. A cafetal extended along the north side of the subdivision. Where a road entered the cafetal, a colony of *Ameiva undulata* was found and many were caught and marked within a radius of 30 m in April 1968. On later visits the small colony on which efforts had been concentrated had been largely destroyed or dispersed as a result of bulldozing. *Anolis cupreus* and *Sceloporus malachiticus* were both present at this locality, but relatively few records of them were obtained. A few horses and cattle ranged over the area. Stray dogs and cats were fairly common, and may have preyed on ameivas in some instances. Brown Jays were seen and heard frequently; otherwise native predators were scarce.

In February 1969 it was belatedly discovered that *Basiliscus basiliscus* was abundant in the gorge of the Río Aguilar immediately south of Las Pavas, and subsequently several visits were made to record population samples from sight records. Sides of the gorge were so precipitous that human activity was largely excluded, and a luxuriant, nearly impenetrable growth of native trees, shrubs, vines and herbs grew there. The bed of the river was boulder strewn, with a series of rapids. The stream was dammed opposite the town, and a cement-lined ditch diverted water from it along the north wall of the gorge. The outer bank of the ditch provided a trail along the side of the gorge, overlooking the river, but becoming progressively higher above it farther downstream. Basilisks on rocks along the river's edge for a distance of about 1 km downstream from the dam were recorded.

Cartago, Cartago Province, 1450-1750 m. This study area was chosen for an investigation of *Sceloporus malachiticus* and

no other lizards were seen on it. Because the lizard population was sparse and the lizards themselves were excessively wary and hard to capture, the study area was extensive and was never precisely defined or limited. Instead, on each visit a somewhat different area was covered—wherever a population sample could best be secured. The area was north of the town, beginning at the west end of the bridge across the gorge of the Río Reventado and extending north along the road toward Bandellira for approximately 2 km. This road paralleled the river gorge, climbing the lower south slopes of Volcán Irazú. The gravelled road meandered back and forth in a wide grassy lane and paths used by pedestrians, horseback riders or cattle paralleled the road or made short-cuts between its loops. Granitic outcrops and boulders were prominent and provided lookouts and shelters for the lizards. Heavily grazed pastures with scattered outcrops and with thickets and clumps of spiny shrub bordered the lane. The windswept slopes also supported small scrubby trees, some isolated and some in compact groves. Sampling extended into the adjacent pastures, especially along a pipeline where rocks were exposed. The pipeline extended west to a flat pasture area adjacent to the northwestern part of the town, which had many boulders and outcrops around its margin. This flat area provided more records than the original roadside strip in late 1968 and early 1969, but in late 1969 it was being utilized for construction of factories and the population of lizards had been eliminated. In January 1970 the original study area along the gravelled road also was found to be grossly disturbed by a road construction program.

During most of the period devoted to the study, there was little disturbance by humans. Many motor vehicles, horsemen and pedestrians passed along the road through the study area, but insofar as known they did not affect the lizard population except by momentary disturbance. Cattle, horses and dogs moved through the area frequently. Stray cats were not seen. Natural predation probably was the one most important factor in eliminating lizards from the study area. Potential predators noted include: the coyote (*Canis latrans*, here at the southern extremity of its range), long-tailed weasel (*Mustela frenata*, several seen), Brown Jay (seen and heard frequently), Broad-winged Hawk and other unidentified hawks. *Thamnophis proximus* was the only snake found on the study area that was large enough to prey on *Sceloporus*.

Turrialba, Instituto Interamericano Ciencias Agricolas (IICA), Cartago Province, 602 m. This area, on a knoll near the Institute headquarters, had trees mostly 0.1 to 1 m in trunk diameter. Low grass and herbaceous vegetation carpeted the ground and was cut periodically. There were a few rock outcrops and large boulders. *Anolis limifrons* was abundant on the tree trunks and often was found on the ground near trees. *Scincella cherriei* was fairly numerous in low vegetation. When the area was revisited on 8 June 1968 it was found to have been devastated by bulldozing and tree-cutting. Most of the trees had been removed and operations were still in progress. Lizards of both species had become scarce. Marking was discontinued and population samples were sought in a new area on the Institute grounds about 0.5 km farther north, in experimental tree plantations. *S. cherriei* was found mainly in leaf litter in a cacao grove and *A. limifrons* was found in more open plantations where there was ground cover of herbaceous vegetation. Other lizards seen in relatively small numbers included *Anolis humilis, A. biporcatus, A. carpenteri, A. lionotus, Ameiva festiva, Lepidoblepharis xanthostigma* and *Basi-*

liscus plumifrons. Anolis biporcatus was found in the same habitat with *A. limifrons,* but was more arboreal and much scarcer. *A. humilis* and *A. carpenteri* were found along the edge of the Río Reventazón. *Ameiva festiva* was found in small numbers in the cacao grove where ground litter was abundant.

Although the experimental plantations and diverse habitats created conditions favorable for lizards, human activity was relatively concentrated, and habitat changes were rapid. Crews of laborers were constantly in the field. Also, there was some use of insecticides on the experimental plots, and at times this may have had devastating effects on lizard populations locally. On 27 Aug. 1969 *A. limifrons* had become much scarcer than on any previous occasions in all the areas when they had been hunted previously.

Dogs were the only domestic animals seen on the study areas and they were not observed to molest the lizards. Brown Jays were often seen and heard. Snakes were probably the most important predators on the lizards, and those found included *Pliocercus annellatus, Drymobius margaretiferus* and *Leptodeira* sp.

Limón, Limón Province, 3 m. The city park was utilized as a study area for the gecko, *Gonatodes albogularis.* A population which must have totalled several hundred lived on about a dozen giant fig trees (*Ficus* sp.). A few others lived on palm trees, rocks or posts, but the fig trees with their massive trunks, buttressed roots, and innumerable holes and crevices were superior habitats. Each tree had its own colony but doubtless there was occasional wandering of individuals from tree to tree. Flower beds, ornamental shrubs and trees of many kinds were present, with wide footpaths having concrete benches along them. Many persons were usually present in the park, the number varying according to the time of day and day of the week. Native birds were fairly numerous in the park, but most of these were small kinds and natural predators were virtually absent.

Portéte, Limón Province, 1-2 m. The study area was a beach resort about 5 km west from Limón, bordering a small bay with semicircular stretch of sand and coral beach several hundred m long. A clubhouse and several cabins were on lots along the beach. A paved road to Limón was inland from the beach 40 to 150 m. The strip between the road and the ocean had groves of coconut palms. Over much of it there were jagged coral rocks, exposed or scantily clothed with vegetation, but part of the area was low and swampy with muddy deposits, hydrophytic vegetation, and often standing water. Rotting piles of old coconut husks were distributed over the area. *Basiliscus vittatus* and *Ameiva quadrilineata* were the species studied, but the latter was much less common and on some visits was not seen at all because of unfavorable weather. *A. festiva* was present where there was relatively dense ground vegetation. *Gonatodes albogularis* occurred on the bases of coconut palms. *Anolis limifrons* was present in small numbers on shrubby vegetation and tree trunks. Human activity probably had little effect on the lizards of the area, though at times there was heavy use by bathers and picnickers. Dogs and a few chickens ranged onto the area, but probably without much effect on the lizards. Snakes were probably the most important predators. Those found included *Leptophis ahaetulla, Rhadinea* sp. and *Pseustes poecilonotus.*

Beverly, Limón Province, 2-4 m. The original study area was located approximately 16 km south of Limón, on the farm of Dan Sargent. This area was essentially a strip 200 m long on both sides of a fence line that separated a marshy pasture from a cacao grove, long neglected and

overgrown with natural vegetation including trees, shrubs, lianas and broad-leafed herbs. The species studied were chiefly *Anolis limifrons* and *A. humilis*, with relatively small amounts of information obtained for *Ameiva festiva, Gonatodes albogularis*, and *Lepidoblepharis xanthostigma*. *Anolis limifrons* was abundant along the fence and at the edge of the field. *A. humilis* was not found in substantial numbers until 23 Jan. 1968; then greater effort was devoted to finding it in the cacao grove, especially around the bases of several giant native trees with buttressed roots. On 8 May 1968 much of the study area had been seriously disturbed by cutting of part of the cacao grove and the natural vegetation growing with it. In compensation the study area was then extended to include a number of large native trees along a sluggish stream adjoining the north end of the original strip. However, on 28 Feb. 1969 the study area including the newer part had been further disturbed by tree-cutting and clearing. Marking operations were then discontinued on the Sargent farm and subsequent population samples were collected about 2 km farther south, in extensive cacao groves immediately north of the railroad stop at Beverly.

ACCOUNTS OF SPECIES

Plan of Presentation

Findings are set forth under a series of species-accounts. The latter are divided by subheadings—*description, range and habitat, general habits, growth, spatial relationships, temperature relationships,* and *reproductive cycles.*

Description in each instance is a highly condensed account mentioning a few of the most outstanding characters of bodily proportions, scalation, color and pattern, and how these vary individually, or according to sex, age or season. Much more detailed descriptions of most of the species can be found in publications such as Taylor's (1956) account of the lizards of Costa Rica. The purposes of my descriptions are: 1) to impart to the uninitiated reader some idea of the sort of animal involved, 2) to indicate sexual or ontogenetic differences hitherto unrecognized or inadequately described, and 3) to enable identification of animals. In view of the possibility of unforeseen taxonomic problems, the descriptions are intended to leave no doubt as to which species were involved in the field work. For most kinds, sizable series of voucher specimens have been deposited in the University of Kansas Museum of Natural History collection. An essential part of the description for each species consists of length measurements (and weights in some instances) listed in Table 2.

Range and habitat. A general statement of geographic range is made on the basis of records in the literature and my own field observations. Peters and Donoso-Barros (1970) have provided a useful reference, but it is evident that details of geographic distribution are not known for any of the species. Habitat is briefly discussed on the basis of my experience with each species on the study areas, more casual observations made elsewhere, and statements from published literature.

General habits. Behavior under natural conditions, daily schedule of activities, extent of basking habit, reactions to humans or other potential enemies, and food habits are considered. Although much of this material will be familiar to biologists who have done field work where the lizards occur, it cannot be found in the literature.

Growth is discussed mainly on the basis of information obtained by capture, marking, release and recapture. However, only a small percentage of the lizards marked were recaptured and the stunting that resulted from handling and marking hindered understanding of the normal growth rate. Injury, parasitism and disease

also affected growth rates, causing individuals to deviate from the usual pattern. Hatchlings that were marked were rarely captured at intervals suitable to show the amount of growth during the early weeks of life.

In the tropics, discrete age groups are often not evident, and growth rate must be measured directly. Knowledge of growth rate was considered essential to an understanding of population structure and of reproductive cycles. The growth rates implied by the age-size correlations in Table 3 were utilized to calculate approximate dates of birth or hatching and egg laying of individuals and cohorts of young. In every species studied growth rate proved to be variable, and while some young made exceptionally rapid growth, others, perhaps handicapped in ways that were not evident, and destined for early elimination, grew little or not at all in weeks or even months. Only those lizards recaptured after "substantial intervals"—when an area was revisited after a month or more—were useful for study of growth. Even after substantial intervals, some that were already adult when marked showed little or no growth. Others, though marked as young, had attained adult size and stopped growing before recapture. Hence relatively few of the 2294 records of recaptured lizards were of significance in showing growth, and these had to be used selectively.

Spatial relationships were investigated by direct observation on the behavior and movements of individuals, and especially by the recapture of marked lizards, which usually were not at the exact spot of the original capture. The movements involved in travel between points of capture were of various types such as escape dash, normal activity within an established home range, gradual change of home range over an extended period, shift to a new home range, or wandering for any of a variety of reasons. Most lizards probably have home ranges of sorts but these may be ill-defined or ephemeral, and they differ greatly in size, shape, and manner of use according to the habits of the species. One objective of the study was to determine the nature of such areas and to compare them in different species. The essentials of a home range for some kinds are a secure hiding place (or several alternative refuges) to which the animal retreats at any alarm, and a nearby look-out (or several look-outs) from which the lizard awaits its prey. The home range of such an animal is not readily definable because intensity of use decreases rapidly with increasing distance from the activity center, and records are usually concentrated near the center. However, certain other lizards, notably the teiids, are less attached to any particular spot and range more freely over a familiar area in an active search for food. For such species the data are best adapted to calculate home ranges by the method of equating average distance between points of capture with home range radius (Fitch, 1958b:73). If the home range is covered uniformly, individual movements recorded should form a graduated series from zero up to a maximum range diameter, with a few much longer movements representing shifts. (See Figs. 7 and 11.)

Temperature relationships were investigated in many but not all of the species by taking body temperatures and adjacent air temperatures at the time of capture demonstrating a somewhat different level of preference and range of body temperature in each species.

Reproductive cycles are discussed partly on the basis of proportions of adult females that are fecund at different times and the stage of reproduction represented by the gonads of those dissected. Also, the seasonal distribution of hatchlings and older young was taken into account to judge the relative level of reproductive ac-

tivity at different times of year. Lizards that were of hatching size or only a little larger showed by their occurrence and relative abundance approximately when hatching took place. For kinds in which normal incubation period was adequately known, times of egg-laying could be calculated for each hatchling. Knowledge of growth rates permitted similar projections of data to calculate an approximate hatching date and egg-laying date for each partly grown juvenile. Of course, incubation periods and growth rates are subject to fairly wide variation, even in one species at one locality, and the older the individual, the greater the range of error in extrapolating back to the date of hatching and of oviposition. However, the expected margin of error is usually small in terms of the annual cycle. The different approaches sometimes produced somewhat conflicting results, with unconformities resulting from the sources of error mentioned above, and also from inadequate samples.

For the sake of brevity, the following conventions are used throughout: "length" =snout-vent length in millimeters; temperature figures=degrees Centigrade; "KU"=University of Kansas Museum of Natural History.

TABLE 1. Kinds and numbers of field records, and localities, for various species.

Species	Number processed, marked and released	Number of recaptures	Number processed without marking	Number recorded as size estimates without capture	Localities†
Gonatodes albogularis	374	47	37	820	B, BB*, L**, P, PDC, Q, S
Lepidoblepharis xanthostigma			5		B, SM, T
Anolis biscutiger			83		Q*
A. cupreus	2542	820	449		BB*, C, FT, LI**, LP, PDC, Q, S**, SJ**
A. humilis	316	45	128		B**, SM**, T
A. intermedius	284	97	30		C, HEP, SJ*
A. limifrons	980	264	688		B**, P, SM, T**
A. lionotus	37	10	5		SM*, T
A. sericeus			18		BB, LI, PDC, Q, S
A. tropidolepis	428	185	50		HEP**
Basiliscus basiliscus	129	28	56	778	BB, FT**, LI**, LP, Q, S
B. plumifrons	3	1	6		B, C, P, SM
B. vittatus	165	35	9	337	B, P**
Ctenosaura similis	153	13	2	745	BB**, FT**, LI, PDC*, Q*, S
Iguana iguana	4		14	35	BB, FT*, LI, PDC, Q, S
Sceloporus malachiticus	226	19	92	715	C**, HEP, LP, SJ*
S. squamosus			12		PDC, S
S. variabilis	1005	374	10		BB**, FT, LI, PDC**
Gerrhonotus monticola	6				HEP
Ameiva festiva	6	1	7	53	B, P, T
A. quadrilineata	21	4	5	712	P, Q*
A. undulata	160	49	3	251	BB, FT, LI*, LP*, PDC, Q, S*
Cnemidophorus deppii	1117	244	1	704	BB**, PDC**, S
Mabuya mabouya			3		B, P
Scincella cherriei	159	58	29		B, Q, T**

† B=Beverly, BB=Boca de Barranca, C=Cartago, FT=Finca Taboga, HEP=Hacienda El Prado, L=Limón, LI=La Irma, LP=Las Pavas, P=Portéte, PDC=Playas del Coco, Q=Quepos, S=Sardinal, SJ=San José, SM=San Miguel, T=Turrialba.

* Sources of moderate amounts of information.

** Sources of relatively large amounts of information.

Table 2. Sizes* of lizard species studied.

	Largest adult ♂ (or ♀)			Typical adult ♂			Typical adult ♀			Smallest reproductive ♀			Typical hatchling		
Gonatodes albogularis	48	65	2.5	43	56	2.0	42	45	2.2	35.5	39	1.2	18	19	.1
Lepidoblepharis xanthostigma	41	49	(♀)	37	46		38	46		34	41				
Anolis biscutiger	43	83	1.5(♀)	39	80	.99	40	78	1.05	33	63	.8	17	32	.14
	41	84	1.1(♂)												
A. cupreus	52	93	2.5(♂)	47	84	1.8	39	70	1.4	35	60.5	1.0	18	27	.2
A. humilis	44	69	2.2(♂)	38	60	1.3	40	76	1.8	32	62	.7	16	24	.15
A. intermedius	54	85	3.0(♂)	48	77	2.0	47	74	2.1	38	62	.9	18	27	.15
A. limifrons	45	92	2.0(♀)	39	81	1.4	40	81	1.5	33	66	.9	17	33	.14
	43	92	1.7(♂)												
A. lionotus	85	148	(♂)	79	140		69	113		60	100		23	35	
A. sericeus	52	114	2.4(♂)	44	95	1.6	41	84	1.23	36	72				
A. tropidolepis	59	108	4.0(♂)	53	102	3.5	52	84	33	42	67	2.0	20	35	.2
Basiliscus basiliscus	228	565		215	534	250	150	318	93	117	303	45	43	90	1.7
B. plumifrons				194	520					113	326				
B. vittatus	145	420	90	134	387	70	115	314	42	86	237	15	39	87	1.5
Ctenosaura similis	440	800		415	675		335	515		212	382		57	130	
Iguana iguana				530	1237		390	920		316	745		60	253	
Sceloporus malachiticus	90	100	(♂)	83	95		78	85		64	72		29	29	.8
S. squamosus				50	110		49	104					26	54	
S. variabilis	77	121	16.0(♂)	68	107	11.0	63	83	7.0	44	69	3.2	23	32	.45
Gerrhonotus monticola	87	147		82	135		77	123		63	101		26	68	
Ameiva festiva	115	252		104	220		104	210		77	156		37	70	
A. quadrilineata	82	180		72	151		70	140		58	116		30	57	
A. undulata	119	262		107	225		97	194		79	158		35	67	
Cnemidophorus deppii	93	202		78	160	9.0	70	145	7.0	59	133	4.5	31	67	.7
Mabuya brachypoda	91	150	(♀)	63	107		71	117		62	102				
M. mabouya	90	148	(♀)	73	124		82	135		73	120				
Scincella cherriei	63	101	4.8(♀)	54	90	2.5	55	85	2.7	48	73	1.7	22	30	

* SV Length in mm; tail length in mm; weight in gm.

Species Studied or Observed

Thirty-four species were observed during the course of my field work, but eight of them were observed rarely (some only once) and so nothing of note was found out about them. These were *Sphaerodactylus lineolatus* Lichtenstein and von Martens and *Phyllodactylus edwardofischeri* Mertens from Finca Taboga, *Thecadactylus rapicaudus* Houttuyn from Beverly, *Anolis pentaprion* Cope from La Irma, Boca de Barranca and Quepos, *Anolis biporcatus* Wiegmann and *Anolis carpenteri* Echelle, Echelle and Fitch from Turrialba, and *Anolis capito* (Peters) and *Corytophanes cristatus* (Merrem) from San Miguel de Sarapiquí. Twenty-five other species were found frequently and in substantial numbers. A twenty-sixth species, *Mabuya brachypoda*, was seldom found in the field, but is included in the species accounts because museum specimens were available for study. Tables 1-3 summarize respectively field records and localities, sizes, and growth for the 25 species most extensively studied. In Table 1 localities marked with a double asterisk provided relatively large amounts of information, those with a single asterisk contributed moderate amounts of information, and those unmarked contributed relatively little because of local rarity or other conditions preventing an intensive population study.

Family Gekkonidae

The two species of geckos included are

both sphaerodactylines. They attain high population densities and are important predators on small arthropods. These lizards are near the minimum size of terrestrial vertebrates. They are short-legged, dull colored, crepuscular and somewhat secretive. They lay spherical eggs with hard calcareous shells, one at a time. The incubation period is remarkably lengthy and the hatchlings are relatively large.

Gonatodes albogularis (Duméril and Bibron)

Description. Small, short-bodied, with short legs and tail, broad head, large lidless eyes with vertical pupils, body flattened, tail cylindrical, skin velvety with minute granular scales, male black with blue dots on sides, orange-yellow head, conspicuous white and blue markings on labial region, and conspicuous white tail tip; female retains juvenile pattern of pale grayish brown mottled with small, irregular blackish areas (Plate IV, lower left).

Range and habitat. Occurs from El Salvador south through most of Central America and northern half of South America, Cuba, Lesser Antilles and Curaçao. In Costa Rica it is limited to low altitudes near sea level but occurs on both coasts, in warm climates ranging from those of the persistently wet rain forest to those with a long and severe dry season and a xerophytic type of vegetation.

The habitat is on tree trunks. Places of concealment, holes and crevices, are essential. The strangler fig with its tangle of roots above ground level, providing a great abundance of hiding places, is well suited to this gecko's needs; large fig trees often harbor sizable colonies of the lizards, and the local distribution may be in part determined by the availability of fig trees. Many other kinds of trees are utilized however, especially those having rough bark in large, loose flakes, having trunks forked with narrow crevices between them, or having small cavities such as those made by large insects, or those having holes beneath the roots. Man-made struc-

TABLE 3. Typical early growth: lengths of young from hatching to 10 months.

	Hatchling	1 month	2 months	3 months	4 months	5 months	6 months	7 months	8 months	9 months	10 months
Gonatodes albogularis	18	22.7	26.2	29.5	32.6	35.5*	38.2				
Anolis cupreus ♂	18	23	28.5	33.5	38	42	45.5				
♀	18	23	28	32	35*	37.5	39				
A. humilis	16	20.5	25	29	32.5*	35.5	38				
A. intermedius	18	24	29.5	34.5	39*	43	46				
A. limifrons	17	24	29	32.7*	36	38.7	40.2				
A. tropidolepis	20	23.8	26.5	29.1	31.6	34.0	36.3	38.5	40.5	42.3*	43.9
Basiliscus basiliscus	43	59	70	79	87	94	100	105	109	113	117*
B. vittatus	39	52	62	70	76	81	86*	90	94	98	101
Ctenosaura similis	57	69	80	90	100	110	119	128	137	146	155
Sceloporus malachiticus	29	37	44	52	55	60	64*				
S. variabilis ♂	26.5	30.5	36	41.5	45.9	55.3	60				
♀	26.5	30.5	36	41.5	44.4*	47.3	50.2				
Ameiva quadrilineata ♂	30	43	50.4	53.4	56.4	59.4	62				
♀	30	43	48.6	52.0	54.0	56	58*				
Cnemidophorus deppii ♂	31	40	46	54	60	66	72				
♀	31	38.5	43	48	53	58*	62				
Scincella cherriei	22	27	31.5	35.5	39	42	45	48*	51		

* Approximate minimum size of female at sexual maturity.

tures including fence posts, especially those retaining bark but having it warped and separated from the wood beneath, stone walls, concrete foundations of buildings, logs and trash are utilized. In most instances these geckos have been seen between ground level and an elevation of about 4 m.

General habits. This gecko is scansorial, and during periods of activity it darts about, over vertical or inclined surfaces of tree trunks, stalking its insect prey. It is mainly diurnal, but activity is concentrated in late afternoon, beginning about sunset, or considerably earlier when places of foraging are in deep shade. Each individual has its own small area of tree trunk with home ranges or territories of a few square meters at the most. At any sudden movement the shy and furtive geckos dart into holes or crevices and disappear. Usually the dash for shelter is only a few centimeters. If routed from its shelter, the gecko most often runs spirally around the tree trunk to another refuge, and disappears within a second or two. Interactions between individuals are marked by frequent pursuits of the smaller by the larger. Predation of large individuals on small ones seems probable. A tail-waving display by adult males serves as a territorial signal, and probably each adult male controls a definite area and excludes other adult males from it. However, holes and cavities that provide the best retreats are sometimes used by groups of individuals and seem to be communal property.

On the Marbella Hotel grounds at Boca de Barranca trunks of two large tamarind trees were known to harbor six to ten individuals each but in general the population was well dispersed, often with only one or two individuals per tree trunk or fence post. In contrast, at the Limón city park, each of the many large fig trees harbored a sizable colony, perhaps several dozen in some instances. The lizards were so abundant that interactions between them were almost continual at times when they were active. Aggression or escape accounted for much of the activity. In this urban situation the geckos were largely free from natural enemies such as snakes, larger lizards and predatory mammals, resulting in unusually high density and intensified intraspecific competition.

Growth. Fifteen of the geckos that were marked at Boca de Barranca were recaptured after intervals appropriate to show growth. For the 9 best records, gains in length were 20 to 26 in 57 days, 25 to 29 in 49, 28 to 33 in 43, 30 to 38 in 85, 28 to 36 in 57, 33 to 41 in 130, 22 to 33 in 95, 34 to 46.5 in 178, and 33 to 43 in 352. The last in this series was a male and the preceding two were females; all the others were of undetermined sex. Relatively rapid growth is indicated, and at an age of six months young have reached the size of sexual maturity. Age-size correlation is shown in Table 3.

Spatial relationships. For 36 recaptures average distance was 9.3 m, extremes 0 to 55 m (see Fig. 7). In 16 instances the gecko was recaptured at the place it was released, or had moved no more than 3 m (within the distance sometimes covered in an escape dash) and was judged to be in the same home range. Most other recorded movements were from 4.6 to 15.3 m over periods of one to 18 months, usually indicating that the lizard had shifted from its original tree or fence post to another nearby. The four longest movements (not shown in Fig. 7) were 52, 52, 37 and 31 m in intervals of 63, 51, 42 and 50 days, respectively. The three longest movements were made by adult males.

Where conditions are favorable an individual seems to remain permanently in the same area of a few square meters and to use the same shelter. Territorial pressure is probably an important cause of shifts, especially in adult males. An en-

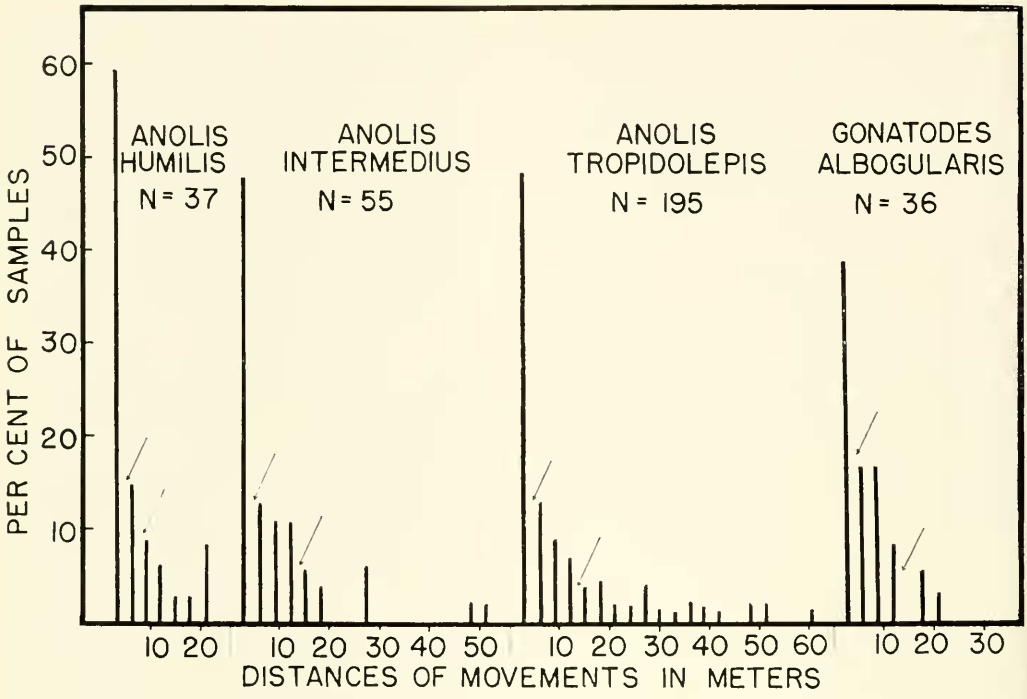

FIG. 7. Distances between points of capture for marked and recaptured lizards of 4 species. Arrows are intended to suggest tentative partial separation of what may be different kinds of movements: short distances within an ordinary home range, medium distances indicating unusually large, elongate, or altered home ranges, and relatively long movements indicating wandering or shift of range.

counter between two adult males, that appeared to involve mutual defense of territories, was observed at Portéte on 30 Aug. 1969. The lizards were on the vertical surface of a rock wall, about 0.4 m apart. Their tails were elevated, and bowed with their tips directed forward over the lizard's backs, and were undulated in a somewhat jerky motion that rendered the white tail-tips extremely conspicuous. From time to time one or the other gecko would rise to an aggressive posture, standing high on its legs, and would sidle jerkily toward the opponent. Heads of both males were lowered, and at times of maximum stress as they came within about 0.3 m, there was a series of peculiar lateral twitching or snapping motions of the heads, which were turned toward the opponents. The confrontation consisted mostly of threat, but once a lizard darted at the other, striking him and perhaps biting him. Each male in turn became the aggressor but with seeming reluctance to move into the area occupied by the rival.

Reproductive cycle. The eggs are white, spherical, hard-shelled and calcareous. Quesnel (1957) found that females of the closely related *G. vittatus* produce eggs at approximately monthly intervals. Eggs of several individuals may accumulate in tree holes and other sheltered places such as those the lizards themselves occupy in periods of inactivity. The incubation period is not precisely known, but judging from the time taken for eggs found in the field to hatch, it is at least four months.

Sexton and Turner (1971) studied a local population of this species at Ancon, Panama Canal Zone, over an entire year and determined the reproductive cycle chiefly on the basis of the numbers of eggs

laid in communal nesting sites over bi-weekly intervals. Ancon is characterized by a dry season, including January through early April, when there is little precipitation, and during this period oviposition almost ceased, but it gradually increased to a peak at the wettest time of year, September and October. Evidence from dissection of females was less clear-cut but tended to bear out the trend of egg collections, as the highest proportion of sexually quiescent females was found in mid-February and greatest numbers of females with oviducal eggs were found in May, June and July. Possibly retention of eggs by females during periods that are unfavorable for laying may alter the results.

In my own study, based primarily upon presence of recently hatched young, and secondarily upon uterine or ovarian eggs or gravid appearance of females, the trend was different. At Limón nine samples averaging 100 lizards each, and well distributed over the year, all included hatchlings and other young up to adolescent size, with no size-group missing from any sample. Obviously egg-laying or at least hatching was continuous throughout the year in this population. The climate of Limón is notably wet, but with relatively little precipitation in February, September and October. The ratio of young to adults did not show well defined seasonal trends in my samples (see Fig. 8). In this urban area growth and reproduction were affected by high population density. Adult size averaged smaller than in other populations and young of all sizes were scarcer. Young up to 32 mm, thought to be in their first four months, were 39.6% of the combined year-round Marbella samples but only 16.9% of the Limón samples. Cannibalism is suspected as a density-dependent mortality factor reducing the numbers of young at Limón.

At Boca de Barranca on the grounds of the Marbella Hotel, ten population samples were obtained by capture-recapture, representing all months except March, September and October. The climate at this locality is comparable to that of Ancon, Canal Zone, with a virtually rainless dry season extending from December into April. Nevertheless, young of hatchling size or but little larger were present in every sample, indicating year-round hatching in this population also. In two August samples young that were less than half grown were poorly represented, indicating (on the basis of an estimated four-months incubation) reduced egg-laying in December, January, February and early March (see Fig. 9). Samples from early January, early and late February and early April had a high proportion of hatchlings and other young, indicating that there is more

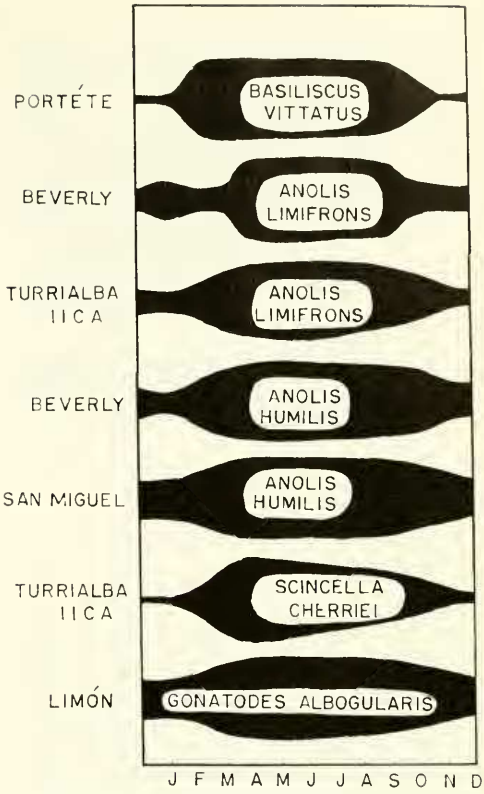

Fig. 8. Relative levels of egg production through the year in 7 lizard populations of the Caribbean versant in areas of high rainfall.

FIG. 9. Relative levels of egg production through the year in 4 lizard populations of the Pacific versant.

egg-laying in September-November than at other times of the year. Females dissected during the dry season invariably had either a large ovarian follicle or a uterine egg. Most of the females obtained were not dissected but were marked and released. When a female had a shelled egg in the oviduct, nearly ready to be laid, it could be discerned through the ventral body wall. In every sample there were some such obviously gravid females.

Lepidoblepharis xanthostigma Noble

Description. Small with short legs and digits, a narrow head, large lidless eyes having round pupils, tail heavy and cylindrical, usually between 1.1 and 1.25 times length; skin velvety with minute granular scales dorsally, and larger, imbricate scales ventrally; color above dark brownish lavender marbled with indistinct lighter areas, and with a pair of white dorsolateral lines distinct in some individuals, faint and/or broken in others, head paler than body; venter light lavender, with brown dots and reticulations on chin; each claw retractile into a compressed sheath.

Range and habitat. Occurs from Nicaragua south through humid lowlands of both Caribbean and Pacific coasts, and at intermediate elevations up to about 1500 m; south to Colombia. Typical habitat is in leaf litter in rain forest, but the species occurs also in altered situations, especially in cacao groves.

General habits. These geckos are secretive and tend to stay out of sight beneath dead leaves even when they are active. Occasionally one flushed by movements of a person is glimpsed darting across an open place.

Reproductive cycle. Like other sphaerodactylines these lay only one egg at a time and the right and left ovaries alternate. Sixty-six specimens (KU) from Costa Rica (mainly north-central part) represent June (8), July (22), August (18) and September (18). Each sample contained gravid females and young of several sizes. The smallest juvenile, collected in July, was 20 in length. If *L. xanthostigma* parallels *Gonatodes albogularis* in incubation and early growth, the gravid females and young of different sizes, found in June, July, August and September, may be construed as indicating egg-laying in every month of the year.

Family **Iguanidae**

This large family is especially well represented in the Neotropical region and includes 16 of the 26 species in the present study. These constitute four phylogenetic and ecologic groupings, anoline, basiliscine, iguanine and sceloporine. The anoles are represented by many species; they are slender, active, mostly small lizards that are primarily arboreal, but with kinds that are secondarily terrestrial (*Anolis humilis*) or even semi-aquatic (*A. lionotus*). Eggs are produced singly with left and right ovaries alternating, sometimes in unbroken sequence when environmental conditions remain favorable. In contrast with many other iguanids, anoles need to drink fre-

quently, are subject to desiccation, and hence tend to be limited to moist situations. The egg is left poorly concealed, or dropped in superficial situations. A notable aspect of anole ecology is widespread sympatry between species with competitive relationships and some degree of habitat partitioning (Schoener, 1968). The species that I studied occurred in various combinations, with two to several at each locality.

The basilisks are medium-sized lizards of riparian habitats, predatory and partly herbivorous. Size differences between young and adults and between adult males and females are unusually great. Growth and longevity are prolonged. The populations studied always consisted mainly of immature individuals.

The iguanines, *Ctenosaura similis* and *Iguana iguana* are notable for their great size, largely herbivorous habits, and clutches of eggs that are near the maximum for lizards. Size difference between young and adults is extreme and attainment of maturity is delayed until the second year or longer.

In the fourth group, the three species of *Sceloporus* are alike in being medium-small, insectivorous heliotherms, but otherwise are ecologically divergent. These are the three southernmost species of the genus, which is widespread in Central America and southern North America. Conforming with a general trend, the montane *S. malachiticus* is viviparous, whereas the two lowland species, *S. squamosus* and *S. variabilis* are oviparous.

Anolis biscutiger Taylor

Description. Small and slender with long limbs (hind reaching anteriorly beyond eye), attenuate tail (about twice length) and head pointed, with frontal concavity; dorsal scales extremely fine and granular, ventrals smooth, two pairs of much enlarged postanal scales; color above, light, yellowish olive, darker in occipital region, ventrally pale, yellowish; obscure dusky bands on legs and toes; some individuals have small median or paired black dorsal spots, widely separated; in some females there is a broad pale middorsal stripe with sharply defined dark edges. Dewlap in male relatively small, whitish with pale yellow at base; absent in female. Adult female slightly larger than male. This species resembles *A. limifrons* in most respects, differing from it only in minutiae of scale characters, color and pattern.

Range and habitat. This little known species was recorded by Taylor (1956:81) from Golfito, Palmar, and near Dominical on the Pacific coast of Costa Rica in southern Puntarenas Province. Williams and Smith (1966) noted two specimens from Julieta, extending the known range 60 km farther northwest along the coast from the Dominical locality. The range is within the tropical humid lowlands of southwestern Costa Rica. I found *A. biscutiger* near Quepos (2.5 km E, 12 Dec. 1967; 1-2 km N, 7 March 1969; 23 and 24 Feb. 1969; 6.5 km NW, 16 Jan. 1968; 10 km NW, 19 June 1968; 0.5-1 km NW Río Cañas, 21 Aug. 1968). It was most numerous along the edge of a recently cleared small field in which beans and corn were growing. The field was bordered by dense thickets and was still littered with logs, stumps and debris, especially along its edges. Elsewhere it was found where there were groves of native trees, often on the trunks among vines and epiphytes, and sometimes on the ground in leaf litter. Also, it was found in small numbers in dense, low herbaceous vegetation in plantations of broad-leafed trees.

General habits. Insofar as observed in the capture of 83 *A. biscutiger* and the unsuccessful pursuit of a comparable additional number, its habits and behavior are like those of *A. limifrons*, which ap-

pears to be a near relative replacing it on the Caribbean versant.

Temperature relationships. On 14 Dec. 1967 and 6 March 1969 a total of 33 body temperatures were obtained from active individuals (Fig. 10). Nearly half of the temperatures were in the interval between 31 and 32 (range 29.3 to 32.5). Air temperatures ranged from 27.3 to 32.6 and were concentrated in the interval between 30 and 31. Body temperature averaged 1.31 degrees above air temperature, and exceeded it in all but one instance. It is noteworthy that body temperatures averaged higher than in the closely related *A. limifrons,* with little overlap.

Reproductive cycle. Samples obtained near Quepos on 12-14 Dec. 1967, 18 Jan. and 1 May 1968, 1 March and 26 Aug. 1969 and 23-24 Feb. 1970 consisted almost entirely of adults and most of the females were gravid, but perhaps egg-laying is suspended or delayed in the dry season. The 26 Aug. sample of 8 included a juvenile of 19 mm and a subadult of 32 mm.

Anolis cupreus Hallowell

Description. Medium-small, long-legged, predominantly brown, with fine granular scales; digital lamellae only moderately developed; tail a little less than twice length; male averages markedly larger than female and differs in having a large dewlap which is amber-orange on

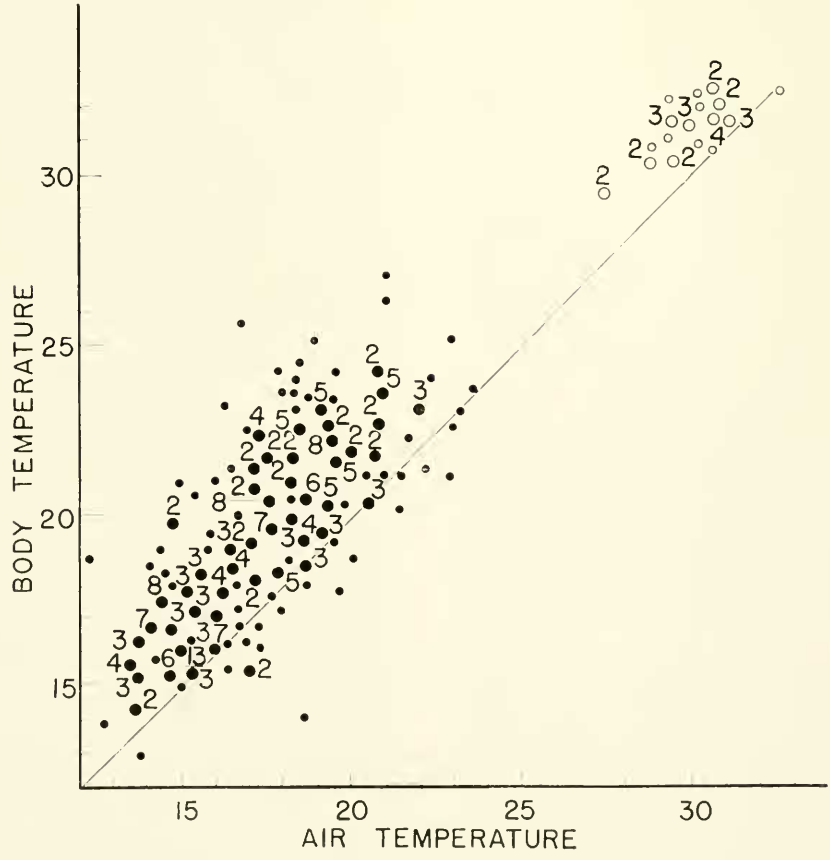

FIG. 10. Body temperatures and adjacent air temperatures of *Anolis biscutiger* (open circles) from Quepos and of *A. tropidolepis* (solid circles) from Hacienda El Prado. Each small circle represents a single record; each large circle represents 2 or more records as indicated by adjacent numbers.

its basal portion and pinkish rose on its outer part. Male often has broad middorsal dirty white stripe bordered by black (Plate IV, lower middle); female pattern usually different and extremely variable, often with a middorsal stripe, which is usually narrower than the male's and may be white, tan, cream-colored or orange, may be reduced to a thin line or may be several scales wide, may be unmarked or may be overlain with a series of chevron-like or diamond-shaped markings; faint, wavy black bars on limbs and tail, variable in shade depending on temperature, light and activity.

Range and habitat. Occurs from Guatemala south into Costa Rica, at low and medium elevations, chiefly on Pacific slope, mainly in northwestern one-fourth of country, east to Cartago and Río Dominical, chiefly in areas having a pronounced dry season. It seems somewhat more tolerant of xeric conditions than are many other anoles.

The habitat is chiefly where there is abundant leaf litter. In the xeric climate of western Guanacaste the species is largely confined to mesic situations along streams where there are large trees and dense shade with leaf litter. The lizards are sometimes fairly common in cafetal, climbing on the coffee trees and utilizing as shelter the brush piles left from the pruning of the trees. They are common along wooden fences or wire fences with wooden posts, especially where there is fairly thick ground vegetation and where the posts are living trees with some foliage, or have some growth of vines or epiphytes. In San José and Cartago large populations have been found in vacant lots, climbing on shrubs, fence posts, buildings or garden walls, or occasionally in thick grass with no objects to climb upon.

General habits. In cool weather it often basks in the sunshine. In hot and dry weather, however, it tends to stay in hiding and ventures out after sunset, foraging even at dusk. Those from higher cooler areas average several degrees cooler body temperature than those in the hot lowlands.

The lizards are partly terrestrial. In the places where they are found, herbaceous vegetation or leaf litter is abundant and one may disappear beneath this shelter in response to danger. Also there are strong climbing tendencies, and a lizard may dash a meter or more to a tree or shrub to escape. On a large tree trunk it usually runs spirally upward. On a shrub, vine or sapling it may ascend keeping the stem between itself and the pursuer, and then crouch, concealed except for its feet which clasp the stem within view.

Populations attain remarkably high densities. Several adults may be found within a square meter, or on the same fence post or tree trunk. The dewlap is especially large in the male and the display is well developed. Presumably there is territoriality of sorts. At San José and Cartago where the lizards were found in large numbers in vacant lots, cafetals and roadsides, males were often conspicuously perched on fence posts which seemed to be territorial look-outs. Search would often reveal a female closely associated with the male, but in a lower much less conspicuous place.

Growth. A total of 820 recaptures of marked *A. cupreus* were recorded, mostly after intervals of several weeks up to 22 months, but many of the lizards were already adults when they were marked, and relatively few represented the early stages of growth. Although numerous hatchlings were marked, only those of 24 mm or more were ever recaptured. High natural mortality, and delicacy of the hatchlings make them difficult to capture without injury and contribute to the difficulty of tracing growth in the early stages.

In 8 recaptured males from San José,

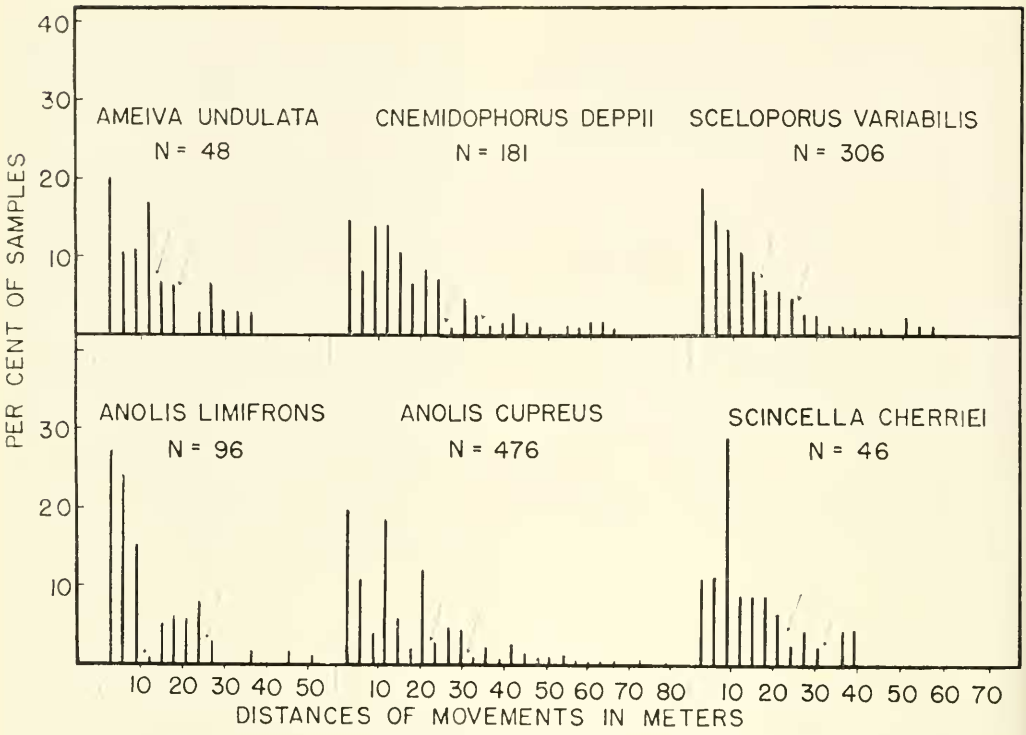

FIG. 11. Distance between points of capture for marked and recaptured lizards of 6 species; arrows as in Figure 7.

Sardinal, and Boca de Barranca, gains in length were 25 to 31 in 17 days, 26 to 36 in 52, 26 to 35 in 89, 24 to 35 in 49, 28 to 35 in 49, 24 to 46 in 200, 27 to 48 in 189, and 33 to 45 to 48 in 267 and 35. In 6 recaptured females from Sardinal and Boca de Barranca gains in length were 25 to 33 to 43 in 49 and 192, 24 to 45 in 41, 28 to 33 to 42 in 12 and 87, 24 to 43 in 150, 25 to 45 in 200 and 29 to 37 in 91. Age-size correlation is shown in Table 3.

Spatial relationships. Compared with the other species of anoles that were studied *A. cupreus* was more vagile, doubtless because of its more terrestrial habits. The longest movement recorded was 210 m and seven others exceeded 100 m (not shown in Fig. 11). However, these were exceptional. As shown in Figure 11, the majority of movements were less than 12 m and nearly one-third of the movements were in the range 12 to 30 m. Inasmuch as the pooled sample of 476 movements includes adults of both sexes and young, from contrasting types of habitats, it could be expected that some individuals would have home ranges much larger than others. Field observations over relatively short periods suggest that in its routine activities an anole of this species normally stays within an area smaller than 12 m across, perching consistently on the same tree or fence post, or staying within a few meters of it when on the ground.

Temperature relationships. Body temperatures of active *A. cupreus* ranged from 18.8 to 34.2, with a continuum between these extremes and no concentration of records that would indicate a preferendum. Air temperatures ranged from 18.4 to 33.6. Maximum body temperatures were recorded in the relatively hot climates of Boca de Barranca and Sardinal (Fig. 12), and La Irma, and at these localities body

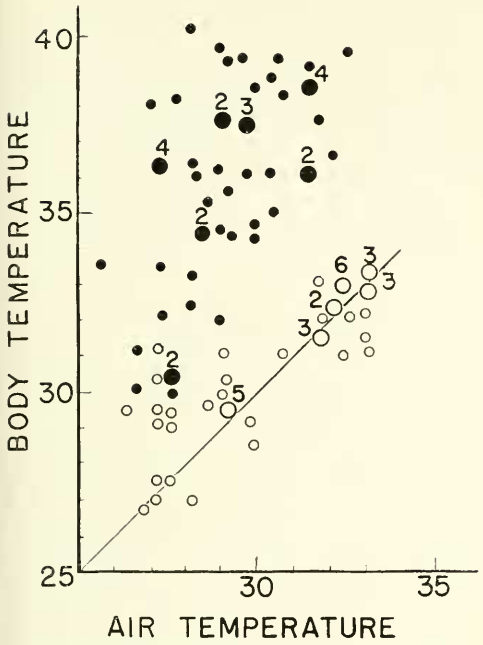

Fig. 12. Body temperatures and adjacent air temperatures of *Ctenosaura similis* (solid circles) from Playas del Coco, Sardinal, and Boca de Barranca and of *Anolis cupreus* (open circles) from Sardinal and Boca de Barranca. Small and large circles show numbers as in Figure 10.

temperatures always approximated the air temperatures of the shaded places where the lizards tended to stay. In the cooler climate at San José the anoles were often observed basking, and their body temperatures were usually higher than air temperatures. However, body temperatures at San José averaged consistently lower than those at lowland localities in warmer climates.

Reproductive cycle. The four populations that were intensively studied all conformed to essentially the same pattern (Fig. 13) with egg-laying extending over about half the year, late April or May through October, and little or no reproduction in the remaining months. The nonreproductive period extends over the entire dry season, which is severe throughout the range of *A. cupreus*; also it includes the beginning and end of the rainy season. At the beginning of the breeding season in late spring the population consists essentially of adults with a few adolescents or large young resulting from late hatch or retarded development. A small percentage of the adults are second-year breeders, but most are still in their first year and still growing. Average adult size increases during the rainy season. Females produce eggs at frequent intervals; for instance, one kept in confinement laid 7 eggs from 15 June to 23 Aug. Intervals between oviposition averaged 10 days but were variable. In some instances the interval was not observed because the egg, well concealed beneath debris in the bottom of the container, was undetected for several days. If the production rate of this female was typical, a female surviving an entire

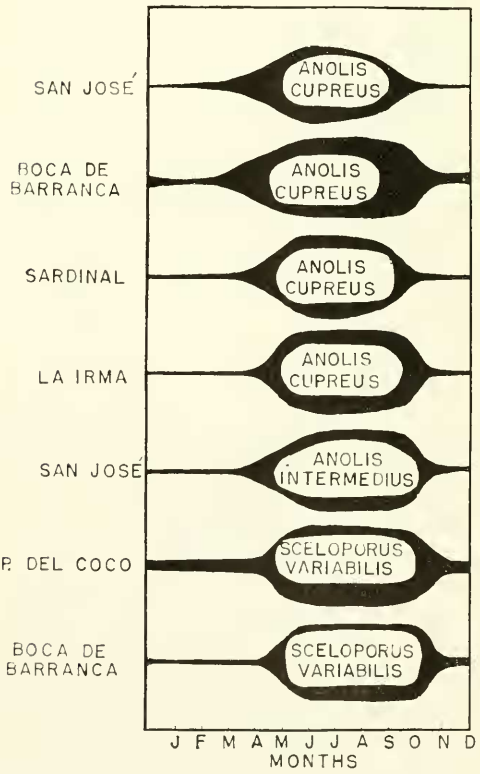

Fig. 13. Relative levels of egg production through the year in 7 lizard populations of the Pacific versant, all in areas having a severe dry season.

breeding season might be expected to produce a quota of at least 18 eggs.

San José has a cooler climate than the other three localities, and collections made in early November and early December are almost lacking in juveniles near hatchling size, but have increasing numbers that are of second-month, third-month and fourth-month size. This distribution seems to show that the season of oviposition was tapering off rapidly in September and October. At Boca de Barranca an early January sample had a few hatchlings indicating that egg-laying had continued well into November. Winter samples from La Irma and Sardinal had young indicating continued egg-laying into early November and late October, respectively. At La Irma and Sardinal hatchlings were appearing in early July, and there were no older young. At San José and Boca de Barranca mid- and late-August samples had young from hatchlings to third month size, indicating that egg-laying began about the same time as at Sardinal.

Many females from various localities, dissected in February and early March, had well-developed fat bodies but their ova were minute. However, in late March and April many of them appeared to be gravid and some of those dissected were oviger-ous. The fact that they were carrying eggs many weeks before actual oviposition occurs, probably means that the fertilized eggs are retained in the oviducts, with development arrested, until environmental conditions favor their deposition.

At Quepos, samples totaling 98 were obtained in December, January, February, March, April and August. The late August sample consisted largely of immatures of graded sizes. The December sample consisted of adults and young that were mostly well-grown, but the smallest was only 24 mm—about 1 month old. The March sample consisted of adults exclusively, and so did the February sample except for one lizard of two-months-old size (28 mm). Thus the seasonal schedule conformed well with that found elsewhere. On 11 March 1970 a series of 78 was collected at Cartago. This series too consisted essentially of adults with the smallest lizard (32 mm) ostensibly representing an egg hatched in late October or early November.

Anolis humilis (Peters)

Description. Diminutive, stout-bodied, relatively short-legged, having 8 or 10 much enlarged rows of keeled dorsal scales; digital lamellae only weakly developed; lateral scales granular; caudal scales large, keeled; color dark, dull brownish olive, sometimes without much pattern and sometimes with a series of connected hourglass-shaped darker brown middorsal marks; a broad V-shaped band across forehead; tail approximately 1.5 times length (often a little longer than this in males and a little shorter in females); dewlap large, deep red with bright yellow outer margin in male, scarcely developed in female.

Range and habitat. Occurs from lowlands of Chiapas, México, south and east through much of Central America, at least through the Canal Zone to eastern Panamá. In general it is confined to low altitudes and warm humid climates and occurs in Costa Rica mainly on the Caribbean slope, but encroaches into parts of Guanacaste and Puntarenas provinces in the Pacific versant.

The habitat is chiefly in tropical rainforest. Often the lizards are in leaf litter, but their abundance centers about the buttressed roots of large forest trees. A colony of a dozen or more may live about a single tree. Where isolated groves or even isolated trees remain, there are often colonies of the lizards. Most that I observed were in cacao plantations where there were occasional large forest trees remaining.

General habits. Activity is strictly diurnal but is in dim light beneath a dense foliage canopy and often under overcast skies or in rain. The radiating buttressed roots of large trees provide surface areas and travelways on which the lizards run, spending much of their time above ground level. Sometimes they have been found more than one meter above ground, but usually they are nearer ground level. They dart rather rapidly over the root buttresses and tree trunks and are not readily distinguished from the geckos that live in the same situations. When alarmed the anoles run in short spurts, often for only a few centimeters, and crouch in sheltered places concealed by low vegetation or ground litter. In the dim light of the habitat they are difficult to see, and after running briefly and stopping suddenly, one may be overlooked and escape.

The large and conspicuously colored dewlap functions in aggressive display. Evidence of territoriality was observed on various occasions when a lizard escaping from me came close to another and elicited the display, but actual combat was not observed. Those that were recaptured after the longest intervals were still at approximately the same spots on buttressed roots.

Growth. Of 35 marked and recaptured after intervals of weeks or months, 20 had made substantial growth. Ten of these are considered most representative. For the 3 males gains in length were 24 to 29 in 44 days, 29 to 36 in 123, and 33 to 38 in 82. For the 7 females gains in length were 18 to 31 in 106 days, 23 to 37 in 118, 28 to 38 in 82, 27 to 40 in 218, 29 to 34 in 46, 34 to 38 in 82, and 37 to 41 in 123. Age-size correlation is shown in Table 3.

Spatial relationships. Anolis humilis was the least vagile of all the species studied (Fig. 7); most of those recaptured were within a few meters of the original site—often on the same tree trunk or root buttress, even after several months.

Temperature relationships. Eighteen body temperatures were obtained, on four different dates at Beverly and San Miguel. All were in the range 20.0 to 26.9 (Fig. 14). In most instances the body temperature was within one degree of the air temperature and greatest deviation was 1.6. Obviously these lizards are non-baskers as sunlight is scarce in their forest habitat. Body temperature is controlled by a combination of substrate temperature and air temperature. Although the records are too few and too variable to indicate a preferendum, it is obviously somewhere in the range 22 to 27 degrees that encompassed most of the records, remarkably low for a tropical lizard and for an anole. Most species of *Anolis* that have been studied have preferenda in the range of 27 to 33 (Ruibal, 1961; Jennsen, 1970; Ballinger, Marion and Sexton, 1971).

Reproductive cycle. Nearly all adult females appeared to be gravid regardless of time of year. Seventy-seven were dissected, and all were found to be carrying eggs. Of these gravid females 47.5% had a uterine egg on each side; 29.5% had a

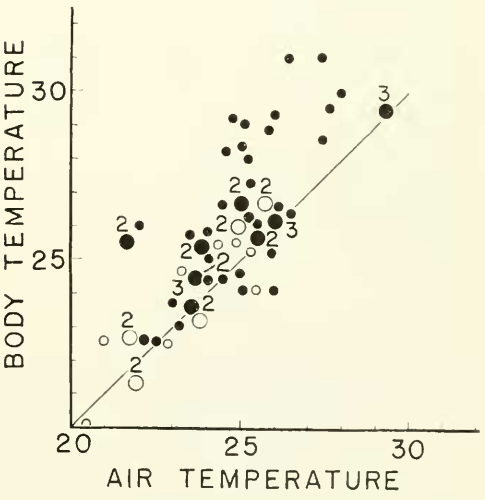

Fig. 14. Body temperatures and adjacent air temperatures of *Scincella cherriei* (solid circles) and *Anolis humilis* (open circles) from Beverly. Small and large circles show numbers as in Figure 10.

uterine egg on one side and a large ovarian follicle on the other; 9.0% had an enlarged follicle on one side only; 7.6% had enlarged follicles on both sides; 6.4% had a uterine egg on one side but no enlarged follicles. In the January-February sample of 13 gravid females 8% had two uterine eggs, as contrasted with 56% (of 25) in March, 57% (of 21) in June, and 44% (of 18) in July-August. No samples are available for the months of September through December.

Evidence of year-round breeding, but with seasonally changing levels, was provided by the distribution of hatchlings and other young. In the 15 population samples from Beverly and San Miguel there were young representing hatching in every month of the year. There were substantial numbers of hatchlings in each sample. Young judged to be less than three months old made up 36.4% of the combined samples. Numbers of hatchlings were relatively low in most January to April samples, bearing out the evidence from gravid females that the rate of reproduction is somewhat slackened during the early months of the calendar year (Fig. 8).

In 12 of the gravid females that had an ovum in each oviduct, the two eggs appeared approximately equal in size, but in the other 25, one egg was definitely larger. Presumably the interval between successive eggs is variable but usually short. A gravid female captured at Beverly on 30 Aug. 1969, laid two eggs overnight, both of normal appearance.

Anolis intermedius Peters

Description. Small, pale greenish olive, somewhat flattened, having medium-short limbs (hind, adpressed, reaches to midneck), toes expanded distally to broad lamellae, ventral scales keeled, tail relatively short and blunt-tipped (usually 1.5-1.7 times length); four pairs of large brownish dorsal spots often discernible, sometimes prominent, on body. Some females have broad, cream-colored or occasionally orange dorsal band with dark edges, but many lack it and are similar to males in color and pattern; dewlap dull white in male, lacking in female.

Range and habitat. Occurs from Nicaragua across Costa Rica to Panamá, at middle and high altitudes, on both Pacific and Caribbean slopes. Upper and lower limits not precisely known, but main abundance is between 1200 and 1800 m. Found on Continental Divide between Cartago and San José; abundant in and near San José, but mainly about eastern part of the city. Not found in the western part of the city nor in nearby suburbs of Escazú and Las Pavas; evidently it drops out or becomes rare as the climate rapidly becomes warmer and dryer to the west.

Trees or large bushes provide the essential part of the habitat. Arborescent plants with small leaves and a thick tangle of stems, preferably thorny, provide a type of habitat that the lizards often frequent. Sometimes massive trunks of large trees are used, especially when there are epiphytes offering effective concealment. Yucca, planted in rows along borders of lawns, roads or property boundaries, are common in central Costa Rica and are especially favored.

General habits. A. intermedius is essentially arboreal. Most of my records are of individuals climbing between 0.3 and 2 m above the ground, but occasionally those pursued have climbed much higher in trees, and also at times they have been seen moving about on the terminal twigs or even the foliage of trees. Several may occur together within a space of a few square meters. Territoriality, if it exists, is of a primitive sort with no rigidly defended boundaries, but with extensive overlapping, and perhaps subordinate individuals are tolerated in the areas de-

fended by those that are dominant. *A. intermedius* has a stereotyped, well-developed display involving spreading the dewlap, but the dull whitish dewlap is far less conspicuous than those of most other species.

A. intermedius is less swift and active than some other species, but it is an accomplished climber. When disturbed, one may dart around to the opposite side of a post or tree trunk, and in doing so tends to move higher, but it may move downward if there is thick cover at or near ground level. In San José and vicinity, where most observations on this species were made *A. intermedius* gave the impression of having much more effective cryptic coloration than *A. cupreus*. When slightly disturbed the lizards have the habit of crouching, flattened against the substrate, and usually their dull surface with grayish or brownish colors renders them inconspicuous. Having climbed as high as possible on a shrub or small tree and still not escaped pursuit, the lizard may turn and run down again to seek concealment on the ground. One that is closely pursued as it climbs often will make a flying leap to the ground and attempt to conceal itself in low vegetation there.

Growth. Marked *A. intermedius* were recaptured from one to five times after substantial intervals, and 32 had made some growth. Most of them represent the middle and late stages of growth, and only one represents the first few weeks after hatching. In 10 recaptured at San José gains in length were 27 to 35 in 45 days, 21 to 26 in 43, 32 to 36 in 42, 32 to 43 in 117, 35 to 44 in 53, 35 to 39 to 46 in 32 and 88, 29 to 44 in 95, 33 to 45 to 48 in 53 and 35, 37 to 48 to 50 in 53 and 29, and 45 to 52 in 86. The first in this series was of undetermined sex, the last four were males and the others were females. Most growth periods overlapped both dry season and rainy season. Tentative age-size correlation is shown in Table 3.

Spatial relationships. Fifty-five recaptures, after an average interval of 45 days, showed movements up to a maximum of 50 m (Fig. 7). Movements averaged 9.5 m. Half were less than 6 m and only two exceeded 27 m. Observations on individuals indicate that one often remains in the same small tree for days at a time, using it as a temporary home range, but that eventually it may shift to another tree or shrub and may occupy a series of them in succession. Nine lizards moved distances of 19 to 27 m to shift from one favorable habitat feature to another. An *A. intermedius* that is well established in favorable habitat probably ranges only a few meters at most from its activity center.

Temperature relationships. Body temperatures ranged from 17.4 to 33.7, but with a preferendum between 25 and 28. Most of the records were obtained from the vicinity of San José (Fig. 15). Fifteen records were from the relatively cool climate in the vicinity of Hacienda El Prado and Vara Blanca on the Continental Divide. These latter records conformed with the general trend of the San José records except that three of them (17.4, 18.2, 18.5) were lower than any in that series. In every instance the recorded body temperature was higher than air temperature; in several instances the difference was less than one degree, but differences of one to three degrees were most common. Air temperatures at which anoles were found active ranged from 15.2 to 28.1, with not much overlap between the two main areas (15.2 to 20.1 for Vara Blanca, 18.4 to 28.1 for San José). Most records were in the range 19 to 26.

Reproductive cycle. Samples were obtained from San José in every month except July and October, and each sample had some females that were obviously

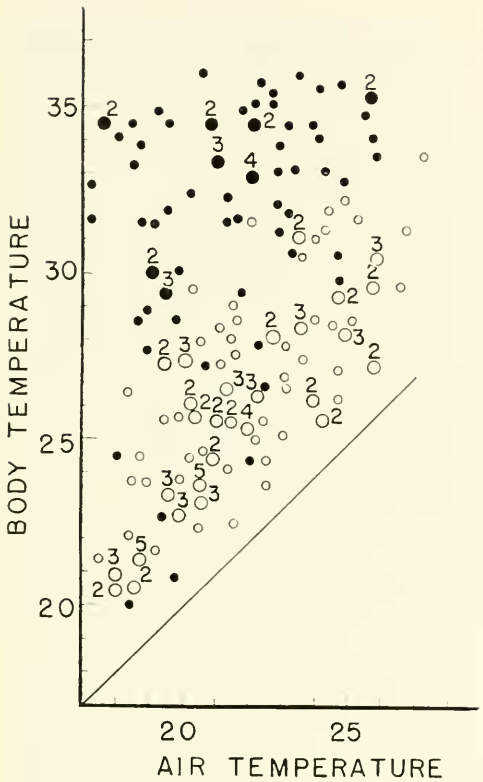

FIG. 15. Body temperatures and adjacent air temperatures of *Sceloporus malachiticus* (solid circles) from San José and Cartago and of *Anolis intermedius* (open circles) from San José. Small and large circles show numbers as in Figure 10.

gravid. Relatively few were gravid in November, but the ratio increased slowly from December to March—a period corresponding with the end of the rainy season and the dry season. The small samples from April, May and June, and better samples from August and September show that most adult females were gravid in this period, whereas in samples taken during the opposite half of the year about half the females were nongravid.

A sample of 91 from early December 1967 had a high proportion of small adults and young of all sizes down to hatchlings, indicating reproduction through the summer and fall months. Samples from 17 Jan. through 7 Feb. 1968 (67), and 18 to 31 Jan. 1969 (77) were similar to each other and combined had only one first-month juvenile, 11 second-month young and 21 third-month young—showing that egg-laying was at a high level in September, but was reduced in October and ended in November. February-March samples are available for 1968 (34), 1969 (44) and 1970 (51). The last was notable for having one hatchling and several second-month young, but in each sample the population consisted chiefly of adults and well-grown young, showing that there was little egg-laying in December and January. April-May (20) and June (33) samples in 1968 consisted entirely of adults (except for one 34 mm male on 11 May), showing that the pause in egg-laying continued through February, March and April. A 10-12 Aug. sample of 19 consisted mostly of medium-large adults, but with young of 22, 24 and 32 mm indicating that a new breeding season had begun, perhaps as early as the end of April. In a 5 Sept. sample half were juveniles, from 18 to 33 mm, showing reproduction from early May through the summer.

The combined evidence from the seasonal distribution of gravid females and young indicates that egg-laying begins in April (or early May) and continues at a high level through October, then dwindles to a stop (or a low level) in November (Fig. 13). Presence of uterine eggs in some females during the dry season is difficult to explain. It may indicate that: 1) eggs are sometimes retained for long periods until conditions become favorable for ovipositing, 2) eggs are laid regularly in the dry season but usually fail to develop due to desiccation, or 3) production of eggs continues year-round but is much slowed in the dry season.

The only clue concerning productivity of individuals was provided by a female captured at San José on 7 March 1970 and brought back to Lawrence, Kansas. She laid an egg on 29 March, and died on 15

April with a fully developed, shelled egg in one oviduct. If she had not died, the interval between ovipositions probably would have been about 17 days. At this rate a female might produce 10 to 12 eggs in the six-months annual breeding season. On 11 March 1970, 16 *A. intermedius* were collected at Cartago, all adults, indicating that here also reproduction was curtailed in the dry season. The many field trips to Hacienda El Prado over a 30-month period resulted in only 18 records of *A. intermedius* and none was below adolescent size, so nothing was learned about the reproductive cycle at high altitude. Presumably incubation and growth are greatly retarded by the low temperatures prevailing at Hacienda El Prado.

Anolis limifrons (Cope)

Description. Small, extremely slender with tail round and attenuate, from a little less than twice to 2.25 times length, head pointed, with frontal concavity; limbs long and slender, the hind, adpressed to body, reaches anteriorly beyond eye; scales minute and granular, those of ventral surface usually keeled; color pale olive above, white with yellowish suffusion below, supralabial region whitish; dorsal black marks usually present but variable, sometimes as several scattered middorsal dots and sometimes paired, or, in female, those on each side more or less fused to form a continuous stripe bordering a broader middorsal cream-colored stripe; male dewlap small and dull-colored, whitish, with a yellow suffusion at its base, dewlap lacking in female; tail with a series of sometimes faint dark rings (better developed in male) separated by wider interspaces; limbs and toes with faint dusky and light bars; females average a little larger than males.

Range and habitat. Occurs from Isthmus of Tehuantepec in México southward through Central America beyond Panama Canal; mainly in tropical zone, but also ascends through subtropical, at elevations at least to 650 m. It is most abundant in humid climates but penetrates into some having pronounced dry seasons.

The habitat is in tropical rain forest, but especially forest edge and disturbed situations including plantations, gardens, thickets, groves, and vine tangles. Often the lizards are abundant in cacao groves. They have been found in coastal coconut groves, but only in small numbers as cover is usually inadequate.

General habits. A. limifrons attains a higher population density than any of the other species investigated. It is both terrestrial and scansorial. Slender build and long legs render it a swift and skillful climber, but much time is spent foraging on the ground, sometimes away from any elevated objects. Sometimes they have been found in meadows, foraging in grass and low herbaceous vegetation. In moving about, they sometimes kept above the mat of low vegetation, and sometimes passed through or beneath it. When pursued, they would progress rapidly with a series of froglike hops. The lizard might conceal itself in dense low vegetation, but generally preferred to climb. One flushed might run rapidly up the stem of a shrub or vine for a meter or two, and then spin around facing downward, and flatten against the stem to conceal itself. At a further alarm it might run back down the stem and either hide in ground litter or dash to another shrub or tree trunk. In climbing the lizards are able to run over leaf surfaces.

Growth. A total of 264 recaptures were recorded at Turrialba and Beverly, but relatively few of these constitute significant records of growth, because most had been marked as adults or subadults. In the following records of the 17 individuals considered most representative of normal growth, "B" designates those from the Beverly study area; all others were from

Turrialba. In 6 males gains in length were 20 to 41 in 224 days (B), 21 to 35 in 88 (B), 23 to 37 in 40, 28 to 38 in 82 (B), 30 to 42 in 77, and 31 to 36 in 36 (B). In 11 females gains in length were 17 to 30 to 33 in 77 and 50 days, 17 to 31 in 75, 22 to 35 in 75, 22 to 35 in 79, 26 to 37 in 76, 27 to 38 in 77, 28 to 41 in 54 (B), 28 to 38 to 41 in 52 and 89 (B), 30 to 33 to 37 in 41 and 41, 31 to 40 in 114, and 33 to 39 to 43 in 77 and 40. The first female listed reached breeding size in a little less than four months from the original capture as a hatchling, but five or six months seem to be more typical intervals for attainment of adult size. Differences in growth rate are not evident between males and females, nor between the population in the tropical climate of Beverly and that in the subtropical climate of Turrialba. Age-size correlation is suggested in Table 3.

Spatial relationships. Records of 96 that were marked and recaptured are available to show movements (Fig. 11). Movements in the neighborhood of 3 to 6 m were most common and the relatively few movements exceeding 24 m probably represent shifts into new areas. The sexes seem to be similar in size of home range and in extent of vagility.

Although objects to climb such as trees, shrubs, fence posts, or vines are important in the ecology of *A. limifrons,* one may have a range which encompasses several climbable objects, and may spend much time on the ground between them.

Temperature relationships. One hundred and twenty-four body temperatures were obtained at Turrialba and Beverly (Fig. 16). Records were concentrated in the range from 25 to 28 which is assumed to approximate the preferendum. In only

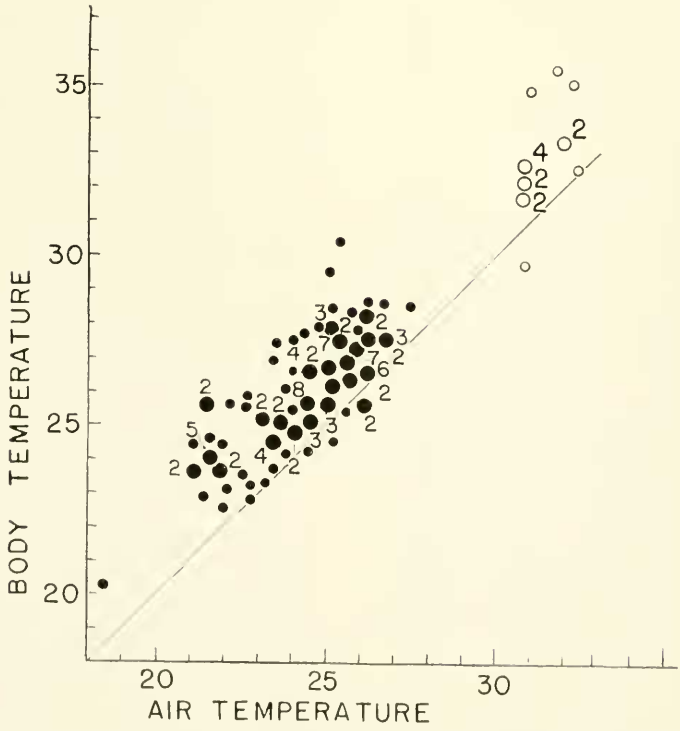

FIG. 16. Body temperatures and adjacent air temperatures of *Anolis sericeus* (open circles) from southern México and Guatemala and of *Anolis limifrons* (solid circles) from Turrialba and Beverly. Small and large circles show numbers as in Figure 10.

five instances was body temperature lower than air temperature, and in each of these the difference was less than one degree. In all other cases body temperature was the higher, but usually it was within three degrees of air temperature.

A. limifrons is often exposed to sunshine during the course of its routine activities, but it is not a persistent basker and usually tends to approximate eccritic temperatures. In the warm, moist climate of its preferred habitat, temperature is usually within or near its preferred range so there is little need for behavioral thermoregulation.

Reproductive cycle. A total of 150 adult females (90 from Beverly and Portéte, 60 from Turrialba) in 16 different samples were dissected, and in each sample the majority of females (79.1%) had a uterine ovum on one or both sides. These females represented the months January through April, June, and August. Six different reproductive categories were recognizable, as follows: 1) uterine eggs on one side and enlarging ovarian follicle on opposite side (57.4%), 2) egg in each oviduct (16.0%), 3) enlarged follicle on one side only (7.9%), 4) nonreproductive (6.0%), 5) ovarian follicle on each side (5.3%), 6) egg in one oviduct (7.4%). The changing ratios of these categories showed no clear-cut trends from one sampling period to another, or between the localities. In three instances (in early March and late August) a large female with two uterine eggs had also an enlarged ovarian follicle on the same side as the more advanced ovum. The simultaneous occurrence of three reproductive units in the oviducts and ovaries might indicate accelerated reproduction with shortening of the interval between ovipositions, or it might indicate merely a retention of an egg ready to be laid, with concurrent development of a new follicle. Alternation in ovulations by the left and right ovaries is indicated by the fact that the majority of females had an enlarged follicle on one side and a uterine egg on the other, or if both oviducts contained eggs, these were often of different sizes. The more advanced egg might be already shelled, but a female never contained two shelled eggs simultaneously. Relative bulk of the larger and smaller eggs varied widely between individuals, indicating that intervals between ovipositions are highly variable. Perhaps the rate of maturation of eggs changes also, according to weather, food supply or other factors. Evidence from the females dissected and from a much larger number examined and released indicates that reproduction is continuous throughout the year.

The changing ratios of hatchlings and other young in the population provides a basis for judging the seasonal distribution of ovipositions. At Beverly hatchlings varied from 41% of the October 1967 sample to less than 1% of the March 1970 sample. The high ratio of young up to 26 mm long in the October sample indicates peak production in August and early September. Abundant young up to 32 mm in late August and early September samples also indicate high production from late April to early July. In five March to June samples the ratios of young are lower, indicating some slackening of the rate of reproduction from mid-January to early May.

At Turrialba the population samples showed a similar seasonal trend with high ratios of young in June, August and especially November, indicating reproduction at a high level from mid-March through October, and with much fewer young in January through April samples indicating a reduction in rate of reproduction from December into early March (Fig. 8). The sample size varied from 46 to 218 and averaged 116, but much larger samples would be necessary to measure precisely the frequency of occurrence of any given

age class. Anyhow, the ratios of hatchlings and of other young varied unpredictably. For instance, within the period 20 Feb. to 18 March in three different years percentages of hatchlings in samples at Turrialba were 18.4, 7.6 and 2.3% and at Beverly were 14.4, 7.1 and 0.7%. Varying weather and changes in local habitat from year to year are thought to be more important than small sample size in causing such variation.

Sexton et al. (1971) observed year-round changes in the reproductive organs of male and female *A. limifrons* at several localities in the Isthmus of Panamá. Five localities were near the Pacific end of the Panama Canal, where annual precipitation averaged 1779 mm, two were near mid-Isthmus where precipitation averaged 2729 mm, and two were near the Caribbean end of the Canal where precipitation averaged 3140 mm. All localities had much reduced precipitation from about mid-December to about mid-April but drought was much less severe on the Caribbean side and at mid-Isthmus than on the Pacific side. The authors found that in the dry season reproduction is virtually at a standstill on the Pacific side (most females lacking enlarged follicles and oviducal eggs) and is somewhat reduced at mid-Isthmus and the Caribbean side. In males, testis weight decreased during the dry season but mature spermatozoa were always present. It should be noted that Isthmian *A. limifrons,* compared with the Costa Rican populations studied by me, are larger, have larger more highly colored dewlaps, and are perhaps subspecifically or even specifically distinct.

Anolis lionotus (Cope)

Description. Medium large, semi-aquatic, having elongate body and tail and medium limbs (hind extends forward about to level of eye) and relatively short muzzle; about 20 rows of enlarged dorsal scales, some slightly keeled; ventrals enlarged and heavily keeled; postanal scales somewhat enlarged; tail slightly compressed; dorsal color olive with faint dusky bands on body, limbs, and toes, and black, white-edged bands on the tail; a pair of cream-colored lateral stripes arising behind eye on each side and passing through ear, above front leg back to groin, bordered by darker olive areas; under surface cream-colored with yellowish (or in some adult males, salmon-colored) suffusion; dewlap in male large, light orange; lacking in female.

Range and habitat. Occurs from Chontales, Nicaragua through much of Costa Rica, and at least to Cocuyas de Veragua, Panamá. In Costa Rica it occurs in the tropical and subtropical zones chiefly at medium-low elevations, but perhaps is not widespread on the coastal plain, preferring swift mountain streams. It was usually found perched on a rock in a stream, or else in the relatively barren rocky riparian zone below high water mark. Occasionally, individuals were seen in dense vegetation but always within a meter or two of the edge of the water.

General habits. This anole is partly aquatic and spends nearly all its time at the edge of the water. The dark color and immobile stance cause the lizard to blend with the surroundings so it is not highly conspicuous. It enters the water without hesitation, and swims and dives easily. Upon approach of a person the lizard usually flushes at a distance of several meters, and moves towards a more sheltered place. Usually the dash is short (often less than 1 m) and the lizard runs over rocks on shore and through the water indiscriminately. It may run to a crevice beneath or between boulders, or beneath undercut tree roots, it may dive and hide beneath a submerged flat rock, or it may plunge into the rushing water, and be swept downstream. However, in such cases the lizard

swims vigorously underwater, gains the lee side of a boulder before travelling far, and hides submerged or with only its head protruding.

Growth. From 2 March to 16 April 1968 a young male grew from 39 to 40 mm and another young male grew from 36 to 43 mm. Presumably there was some stunting in both, especially in the first. Maintaining a relatively low body temperature, *A. lionotus* may grow less rapidly than most other anoles.

Temperature relationships. Six body temperatures obtained in the field ranged from 19.2 to 26.2; the lowest one was slightly lower than ambient air temperature, but all the others were slightly higher than air temperature.

Campbell (1971) obtained 13 body temperatures of *A. lionotus* in Panamá, which averaged 26.4 (range: 26.0-26.8). He concluded that both this species and the similar *A. poecilopus* are heliophobic, since over 600 hours of observation failed to produce any records of basking behavior or voluntary exposure to high light intensities. In a laboratory temperature gradient anoles of both species spent most of their time between 26.1 and 28.0.

Reproductive cycle. One female was captured in 1968 on 10 Jan., 1 March, 16 April and 1 June, and was obviously gravid on each of these dates. At least one oviposition might have occurred in each interval, and the four captures span nearly half an annual cycle, suggesting continuous egg production during these 5 months. The lizard was only 60 mm long, minimum reproductive size, on 10 Jan. but had grown to 66 mm, still less than average adult size, on 1 June. A second female was also gravid on 10 Jan. and again on 17 Aug. She was preserved on the latter date and had a fully developed egg 11 x 5 mm in the left oviduct and a follicle 5 mm in diameter in the right ovary. Another female caught on 10 Jan., one on 16 April and one on 17 Aug. were also gravid. Gravid females from Costa Rica (KU) include: 10 from January, 1 from June, and 6 from July. All females longer than 63 mm were found to be gravid.

The gravid condition of females at each sampling period suggests that breeding is continuous, but no records are available for September through December. Young ranging from 31 to 46 mm were fairly common, and were estimated to be mostly in their second or third months. They were captured at the following times: 10 Jan.—31, 36, 38, 46; 18 Feb.—36; 1-2 March —32, 36; 16 April—37, 38, 42, 43, 45; 1 June—45; 16 Aug.—38. There are young of comparable sizes, and some smaller, from January, June, July and August (KU). The best population sample from my study area was obtained on 16-17 April 1968, and contained 20 individuals in a nearly continuous graduated series of the following lengths: 37, 38, 42, 43, 45, 51, 62, 65, 66, 69, 73, 76, 77, 77, 78, 82, 83, 84, 84, 92. Seemingly there had been no extensive gaps when reproduction was not occurring. It is tentatively concluded that in *A. lionotus* in the region of San Miguel, reproduction occurs throughout the year with no important seasonal change.

Anolis sericeus (Hallowell)

Description. Small, slender, with tail usually a little more than twice length, limbs medium (hind, adpressed, extends nearly to eye, and front to anterior part of muzzle); scales fine and heavily keeled, those of ventral surface larger; dorsal color ashy or with bronze suffusion and a silky sheen, with a series of about seven dark middorsal spots on neck and body, variably developed, continued onto tail as faint rings; sometimes a broad, pale middorsal stripe in female; undersurface dull, yellowish white with some dark stippling; faint dusky bars on limbs; dewlap large and well-developed in male, reddish-

orange with large central indigo spot (dewlap small in female with only a trace of bright colors); male somewhat larger and bulkier than female. (See Plate IV, lower.)

Range and habitat. Occurs from Tamaulipas southward to Isthmus of Tehuantepec, and through much of Central America at low and intermediate elevations, extending into Costa Rica on the west at least as far as Boca de Barranca. It is one of the most widely distributed of Central American anoles and occurs in a variety of habitats in forest, savanna, scrub, plantations and gardens. The localities where it was observed in my study represent the southern extremity of the geographic range. The preferred habitat is xerophytic, in woodland of open type or woodland edge or groves. The lizards were usually found climbing on tree-trunks or shrubs. At every locality where *A. sericeus* was found, *A. cupreus* was present in greater numbers, and it seemed that competition between them was reduced by vertical stratification, with *sericeus* generally at a higher level.

General habits. At each of the localities where it was observed, *A. sericeus* was found only occasionally. Uusually it was found on stems or tree trunks 0.3 to 2.6 m above ground level. Some ran to higher levels in escaping, and showed themselves to be skillful and rapid climbers. *A sericeus* is cryptically colored when on a background of tree bark, and like other arboreal anoles it has the habit of crouching flattened against a tree trunk or stem where it is easily overlooked.

Temperature relationships. Body temperatures (of Mexican and Guatemalan specimens that I collected in 1969 and 1970) were clustered in a six degree range, with a preferendum evidently between 32 and 33—notably higher than in most other species of anoles which have been tested (Fig. 16).

Reproductive cycle. Records are too few to show the trend of reproductive cycles but they do show seasonality of breeding. Eleven males and 10 females obtained in February of three different years at Playas del Coco, Sardinal, and Boca de Barranca were all adults (males 38-46 mm, females 35-46 mm). All the females were nongravid. A male taken in April and one in May were also adult. In August the only two individuals observed were a male of 25 mm on 17 Aug. (probably in its second or even third month and hence developed from conception in April or May) and a female gravid on 24 Aug. These few records indicate a breeding season beginning after the end of the dry season, probably in April, and lasting through the summer rainy season, but probably ending in August or September.

Anolis tropidolepis Boulenger

Description. Medium-sized, distinctive in having shortened head and, in adult male, conspicuously swollen tail-base; olive brown dorsally, dull white speckled with black ventrally, having a curved dark band between eyes and another on nape; male usually with series of middorsal black spots or pairs of spots, female often with pale middorsal band or a series of diamond-shaped middorsal marks (but almost unicolor in old individuals); male dewlap medium small, deep purplish red; females lack well defined dewlap, but have chin reddish even when immature; toes but little expanded distally; ventral scales keeled.

Range and habitat. A. tropidolepis is endemic to mountains of central and southern Costa Rica, the Cordillera Central and Cordillera de Talamanca, at altitudes of 1600 to 2600 m.

The habitat is cloud forest, and remnants of cloud forests where logs, snags, stumps, and occasional trees provide elevated situations and support dense growth

of epiphytes. The lizards are nearly always among epiphytes, in places where hollows and interstices provide abundant shelter, usually between ground level and a height of about 2 m. Occasionally they have been found in grass several meters from stumps or trees and have been found several times on eroded banks. In the wet climate of the cloud forest, grass and other low vegetation grow in a spongy mat providing effective shelter much like that of the epiphytes growing on tree trunks and stumps.

General habits. A. tropidolepis lives in a region of relatively low temperature and lacks the thermoregulatory behavior of most lizards. Body temperatures are therefore low and variable. Movements are relatively slow and clumsy compared with those of other lizards, but predators are scarce and hiding places are abundant and readily accessible. At any alarm the lizards disappear beneath screening vegetation and work their way downward through successive layers into cavities or crevices. Occasionally these anoles have been found on fence posts or bare surfaces of logs and stumps, but they do not regularly utilize look-out perches as do various other anole species. Because of the dense vegetation, this anole would usually be unaware of another nearby, and social interactions would occur only rarely, when two happened to meet. In confinement they display vigorously and fight when placed together.

Growth. There is much variation in rate of growth even between individuals of the same size, but growth averages slower than in other species. The rate usually exceeds 2 mm per month and sometimes exceeds 3 mm in young that are less than half grown. Young caught and marked when they appeared to be only a month or less old were recaptured as follows: 43 mm (minimum size of sexual maturity) at eight months, 43 mm at nine months, 46 mm at 11 months, 49 mm at 13 months. Attainment of full adult size, 52 mm, requires at least 15 months. Age-size correlation for an individual making typical growth is suggested in Table 3.

Spatial relationships. As shown in Figure 7, most of those recaptured, even after periods of many months, had moved less than 3 m. Such individuals were usually on the same tree trunk or stump. Movements up to 20 m, often involving a shift from one tree or stump to another, were fairly common. The longest movement recorded was 420 m (not shown).

Temperature relationships. Body temperature ranged from 12.4 to 26.5 in active *A. tropidolepis* (Fig. 10). There were few near these extremes, but the records were rather evenly distributed over the range 15 to 24 with no obvious preferendum. Laboratory tests showed that these anoles are able to feed at temperatures as low as 14 to 15. Air temperatures at times of capture ranged from 12.4 to 23.7, with the greatest concentration in the one degree range between 18 and 19, fairly typical daytime temperature on the study area. Body temperature usually approximated air temperature and was not consistently either higher or lower.

Reproductive cycle. In the area of my study, and probably throughout the species' range, uninterrupted egg production occurs (Fig. 9). Every adult female examined (143, from all months except July, October and December) appeared to be gravid and 21 that were dissected each had at least one oviducal egg. Uusually there were two oviducal eggs or an oviducal egg on one side and an enlarged follicle on the other. The size relationships of the eggs on the left and right sides varied greatly between individuals, implying that the time interval between ovipositions varies. From the records of marked females recaptured on successive occasions when they were unusually distended with eggs and appeared almost ready to lay, evidence was

obtained that an interval of approximately 30 days between ovipositions is typical. Each sampling of the study area demonstrated the presence of young of various sizes, including hatchlings, with no seasonality.

Basiliscus basiliscus (Linnaeus)

Description. Large, slender, long-legged (adpressed hind limb reaching beyond snout), long-tailed (2.0 to 2.6 times length), long-necked, with fine, granular dorsal scales, a short head, and 3 conspicuous dorsal crests arising as skin flaps from the head, body, and proximal part of the tail in the adult male; body crest extending from shoulder to pelvis, supported by 16 vertebral spines, caudal crest serrate, supported by 22 spines; in adult female only a rudiment of head crest is present with body and tail lacking crests; color is dull olive with a series of dark, transverse bands, one on neck and five on body, obscure in adults; a light line extending from below eye to shoulder; undersurface dull white; ventral scales of body smooth, subcaudals heavily keeled.

Range and habitat. Pacific slope of Nicaragua and Costa Rica through Panamá to western Venezuela, Colombia and northwestern Ecuador. It is chiefly tropical but occurs up to an elevation of 900 m; in Costa Rica it encroaches onto the Meseta Central almost to San José. It is partly aquatic and partly arboreal, is abundant along wooded streams, including some that are reduced to a trickle or to scattered pools in the dry season. In more humid climates it is less confined to the regular stream courses, being found on wooded hillsides and in open marshy areas. A typical habitat is a meandering woodland stream with undercut banks exposing root tangles; a dozen or more individuals will be found within a few square meters on logs and debris of a pile of drift, but intervening stretches of the stream may have few or none. Basking places like protruding boulders or logs beside or in the stream are an important requirement. (See Plate II, lower.)

General habits. A young one approached by a person in its usual surroundings at the edge of the water runs across the surface to the other side. Dashes of usually less than a meter are typical when the lizard is in the vicinity of adequate cover, but those flushed in relatively open situations may run farther, moving over the surface of the water with a brisk bipedal trotting gait, either upstream or downstream, without being deterred by swift water or riffles. However, the relatively bulky adults are much less adept than the smaller lizards at running on water. An adult dashing out into a stream rapidly loses its momentum and sinks; then it submerges and swims away underwater. The young swim and dive well, but have a greater tendency to remain on the surface. The dash of a flushed individual is always toward shelter. These basilisks are remarkably shy; a slight movement of a person 30 m or more from the stream may send several scampering toward shelter. Unless the alarm is severe, the lizard usually stops short of actual concealment, pausing at the edge of the thicket or pile of drift to watch.

Individuals vary in shyness, but usually adults are much shyer than young. Adults tend to stay in the immediate vicinity of shelter and at an alarm usually duck into concealment and remain hidden for a lengthy period, then emerge slowly and cautiously. Young are often found in the open and one sometimes can be approached time after time and it only moves away without concealing itself.

These basilisks climb trees both to escape and to forage. One that is flushed while on or near a tree trunk may climb even though abundant hiding places are available at ground level. Movements of a

person below may cause a lizard to climb higher by several stages until it is on the outermost twigs. Then, if sufficiently alarmed, it may plunge into the stream below. A person following the edge of a stream or wading in it may cause individuals in trees along the bank to plunge into the water. Larger ones submerge immediately, but small ones strike the surface with so little force that they do not submerge, and skitter away on the surface. The climbing habit is less common in young than in adults.

Growth. For 10 recaptured, gains in length were 44 to 52 in 35 days, 45 to 57 in 46, 49 to 69 in 52, 49 to 95 in 196, 74 to 81 in 39, 81 to 86 in 39, 86 to 91 in 16, 110 to 133 in 86, 53 to 108 in 331, and 88 to 134 in 322. The last two in this series were females and the preceding two were males; in the others sex was undetermined. The trend of the records suggests that sexual maturity is attained at an age of one year or a little less (while the lizards are still far short of adult size). Males continue to grow longer and attain a much larger size than females. Tentative age-size correlation is shown in Table 3.

Spatial relationships. Only 13 definite records of movements in the marked basilisks were obtained, and distances ranged from 0 to 56 m for intervals that averaged 48 days. However, one female marked as a juvenile and recaptured after 293 days had moved an estimated 116 m.

Immatures that are flushed in the open may make dashes of 25 to 30 m, so their home ranges must be at least this large in diameter. However, each large individual has a refuge toward which it runs when alarmed. Also, adults are more exacting in their requirements, staying much closer to shelter and possibly having smaller home ranges than juveniles.

Temperature relationships. Seventeen body temperatures were obtained, all in the range 25 to 34. Figure 17 contrasts these with body temperatures of *Ameiva undulata* at the same localities. The *B. basiliscus* temperatures averaged several degrees lower with little overlapping. The basilisk temperatures were all from active individuals, caught in the daytime, and not including those known to have been in the water recently.

Reproductive cycle. Ortleb (1965) reported a female found laying 18 eggs at Barro Colorado, Panama Canal Zone, on 24 July, and these eggs hatched after 77 days incubation. Corpora lutea (9 Feb.), uterine eggs (8 and 10 Feb.) and enlarged follicles (24 Aug.) in females from Finca Taboga and La Irma indicated clutches of 9, 6, 4 and 6. Lengths of females were 152, 148, 146 and 133.

The available records clearly indicate seasonal trends. Usually the lizards were seen too fleetingly or at too great a distance to judge their reproductive states. One female seen at La Irma 11 Feb. 1970 ap-

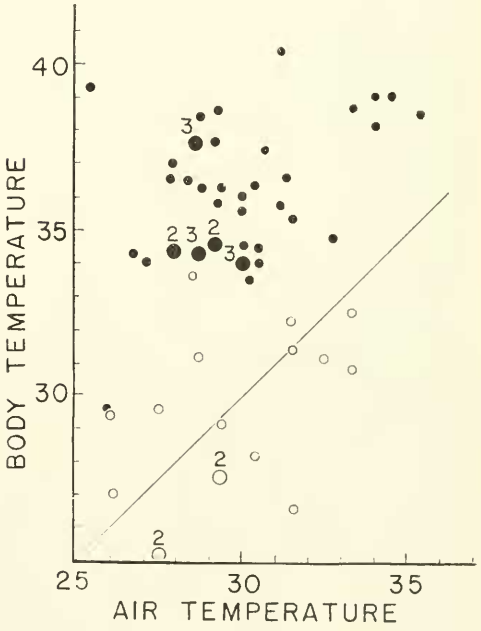

Fig. 17. Body temperatures and adjacent air temperatures of *Ameiva undulata* (solid circles) from La Irma and Sardinal and of *Basiliscus basiliscus* (open circles) from La Irma. Small and large circles show numbers as in Figure 10.

peared gravid, as did another seen there on 16 May 1968 and several seen at Finca Taboga on 18 May and 6 July 1968. However, only nongravid females were recorded at La Irma 1 Feb. 1970 (1 dissected), 9 Feb. 1969 (1 dissected), 19 Feb. 1968 (2 dissected), 23-24 March 1968 (5 dissected), and 1 April 1968 (at least 1 seen). Others were recorded at Finca Taboga 17 Feb. 1970 (1 dissected), 18 March 1965 (11 dissected), 26 March 1968 (at least 11 seen). At Río Naranjo near Boca de Barranca, 10 March 1970, 11 females dissected were all nongravid but had enlarged oviducts indicating recent egg-laying. At an upland locality, Turrúcares (27 km W San José), on 9 March 1970, 2 females dissected were nongravid. These records indicate that most females are not carrying eggs during the dry season.

On every occasion when populations were sampled, young constituted a high proportion of those seen. Uusually they were especially concentrated in one or two size groups, providing a basis for estimating the times when most hatching occurred. Table 4, extrapolating to times of concentrated egg-laying on the basis of dominant size groups of young in 11 large samples from 5 localities, indicates that laying occurs from July to February but is much reduced during the remainder of the year (Fig. 18).

The streambank habitat is subject to drastic alteration when the streams overflow and cut new channels. At such times the eggs may be destroyed in such large numbers that the population structure is altered subsequently, lacking certain age groups of young. In each large sample young of various sizes were present, but certain size classes were especially well represented.

Basiliscus plumifrons (Cope)

Description. Large, slender, fine-scaled; bright green; eye red; conspicuous middorsal crests on head, body, and tail in adult male; head crest double with small anterior part arising behind level of eye, connected at its base with much longer and larger occipital part, body crest arising behind forelegs, low anteriorly but prominent posteriorly, ending just anterior to thighs, supported by dorsal spines of 17 thoracic and lumbar vertebrae, caudal crest confined to basal third of tail, supported by vertebral spines, body and caudal crests with scalloped edges, head crests rounded; limbs and toes long and slender; tail often 2.5 or more times length.

Range and habitat. Caribbean slope of Costa Rica at low and medium elevations, north into Nicaragua and south into Panamá. This basilisk is usually associated with water; both aquatic and arboreal tendencies are marked. At Portéte it was ob-

FIG. 18. Relative levels of egg production through the year in 7 lizard populations of the Pacific versant in areas having a severe dry season.

served in coconut groves, among coral rock and logs at the beach, and along an overgrown concrete wall; at Beverly it was observed in swamp, in cacao, along streams in forest remnant and forest edge. At San Miguel de Sarapiquí and Cartago it was found among boulders at the edge of a swift mountain stream. Hirth (1963a), in his study at Tortuguero, found *B. plumifrons* associated with the more common *B. vittatus*. In commenting on their habitat differences, he stated: ". . . *B. plumifrons* is fairly abundant in trees along the riverbank. It is more arboreal than *B. vittatus* and also is more likely to be found in shaded situations."

General habits. *B. plumifrons* is essentially similar to *B. vittatus* in habits, except as noted above.

Growth. Of several young caught and marked at Portéte, only one was recaptured. At the original capture on 4 Sept. 1968, it had a length of 91 mm. On 30 Jan. 1969 it was recaptured at the same spot and had grown to 113 mm. Presumably growth rate parallels that of *B. vittatus* except that at any given age individuals of *plumifrons* average a little larger and grow a little faster. If so, the one recaptured probably was about seven months old when first recorded.

Basiliscus vittatus Wiegmann

Description. Large, slender, long-legged, long-tailed, with relatively long neck, short head, and fine granular scales; male with conspicuous triangular, middorsal crest, based from behind the eyes to mid-neck, and directed backward; a low inconspicuous crest of enlarged, raised scales along middle of back and extending onto the tail, which is somewhat compressed; in female head crest is represented by a much smaller flap of skin rounded posteriorly, not pointed as in the male; on legs scales are larger than on body, and heavily keeled; ventrals keeled; ground color olive brown, with pale middorsal stripe and a pair of pale narrow dorsolateral stripes arising behind eyes and fading on rear of body; a series of obscure, dark transverse bands on body and tail; undersurface dull white.

Range and habitat. *B. vittatus* occurs in tropical lowlands from Tamaulipas and Jalisco in México through Central America to Colombia and Ecuador. It is present on both coasts of Central America but

Table 4. Time of breeding of *Basiliscus basiliscus* indicated by dominant age classes of young at various time and places in Puntarenas and Guanacaste provinces.

Time of sample	Place of sample	Length of dominant class of young	Estimated age of young (months)	Hatching time indicated	Laying time indicated
late Nov. 1967	F. Taboga	60-70	1-2	Oct.	July-Aug.
late Feb. 1970	Ojo de Agua (850 m, 16 km W San José)	about 80	3	Nov.	Sept.
late March 1968	La Irma	70-89	2-4	Nov.-Jan.	Sept.-Nov.
early Feb. 1970	La Irma	about 60	1	early Jan.	Oct.-Nov.
early Feb. 1970	Río Naranjo (6 km N B. de Barranca)	40-50	0.5	late Jan.	early Nov.
late Feb. 1970	Ojo de Agua	40-50	0.5	Feb.	early Dec.
late March 1968	La Irma	43-63	1	late Feb.	Dec.
Feb.-March 1970	Turrúcares (639 m, 27 km W San José)	40-50	0.5	mid-Feb.	early Dec.
early April 1968	Río Naranjo	about 60	1	early March	Dec.
mid-May 1968	La Irma	44-53	0.5	April-May	Feb.
mid-May 1968	F. Taboga	40-50	0.5	May	Feb.

seems to be absent from extensive areas of the Pacific lowlands in Costa Rica, where there is a pronounced dry season.

It is mainly terrestrial but has aquatic and arboreal tendencies. It lives in rain forest and forest edge, along streams, in swamps, in gardens and plantations. A favorite habitat along the coast is in coconut groves, and the large piles of rotting coconut husks provide the perches and escape shelter that the lizards require. In the groves or adjacent to them jagged coral blocks, logs, beach wrack, tangles of shrubs and vines, and mats of low vegetation also are used for shelter.

General habits. Several authors have described the habits of this species, especially Hirth (1963a) who studied it at Tortuguero in Costa Rica 79 km northwest along the coast from the localities of my study, but in similar beach habitat. Banded basilisks are strictly diurnal and heliothermic. For the night they may climb to perches such as the mid-rib of palm fronds, average 1.4 m above ground (Hirth 1963a), and sleep in the open. Probably some sleep concealed beneath objects also; individuals basking on piles of coconut husks in late afternoon were often observed to retreat into the pile as the temperature dropped and shade fell over them, and they did not reappear.

The lizards are wary, but escape behavior varies greatly according to the situation, the temperature and size of the individual. Flushing distance, as a person approaches, varies from one to 30 m, at least. Typically the aroused lizard makes a dash sometimes as long as 30 m but usually much shorter, taking it away from the approaching person and to or near shelter. If followed, it is inclined to flush again without allowing such close approach as it did at first, and to retreat to a more sheltered situation. An adult that is flushed often ducks out of sight into a hole or other refuge whereas a juvenile sometimes can be approached time after time, and merely retreats without effectively concealing itself. An estimated 10% of the lizards that were flushed ran to trees, usually coconut palms, and climbed beyond reach. More often the lizards ran to or across water in escaping.

Part of the study area, inland from the front dune, was low and swampy and often inundated after heavy rains, with water standing to a depth of 0.1 m. After relatively rainless periods the area lacked standing water but soil was still damp, and the lizards were attracted to such low wet areas.

Hirth (1963a) examined the contents of 320 stomachs from Tortuguero and found a variety of arthropod prey, with tenebrionid beetles, ants, grasshoppers, amphipods, lycosid spiders and lepidopteran larvae especially well represented. In the young the food consisted of animal matter exclusively, but in adults plant food was common, including grasses, seeds, stems and berries. In six adults the stomach contents consisted entirely of plant material.

Since the male is much larger, with highly developed display organs, and since adults tend to stay in certain small areas, it is plausible to assume that these lizards are territorial. However, territorial behavior was not observed either in the course of my field work or in Hirth's study.

Growth. At Portéte 35 recaptures were made after substantial intervals, showing growth. For the 13 considered most representative, gains in length were 46 to 59 to 76 to 86 in 52, 92 and 81 days; 50 to 65 in 51; 54 to 64 in 52; 57 to 64 in 31; 59 to 76 in 92; 64 to 69 in 31; 51 to 78 to 105 in 139 and 232; 53 to 120 in 78; 76 to 84 in 34; 79 to 86 in 51; 49 to 121 in 125; 61 to 113 in 332; and 79 to 98 in 142. The first six of these individuals were of undetermined sex and the last two were females; others were males.

Hirth (1963a) obtained more records for the early stages of growth. For 11 hatchlings (35-40 mm) he found a mean growth rate of 7.5 mm in 15 days and for 16 in the length range 41-50 he recorded a mean of 6.3 mm for the same period. Thus for the first month of life length gain of about 15 mm to a little more than 50 mm may be considered typical. For those of 51-60 mm length he found an average gain of 5.1 mm in males, 5.0 mm in females per 15 days, and in the 61-70 mm group, corresponding figures were 3.9 (♂) and 2.9 (♀) mm. His data were meager for lizards between 70 and 100 mm but my own data are more adequate for this range. The tentative age-size correlation shown in Table 3 is suggested as most typical for males. For females the growth rate is somewhat depressed, especially in the middle and late stages of growth.

In my study the smallest gravid female was 87 mm. Hirth (1963a) recorded one of 83 mm having oviducal eggs, and he recorded males to be sexually mature at a minimum size of 80 mm, but only five of 18 that were 80-89 mm contained spermatozoa. Seemingly sexual maturity ordinarily is attained at an age of about 6 months, but the lizards continue to grow until they are at least twice that age.

One female marked as an adult of 108 mm on 23 Jan. 1968 was recaptured on 12 June 1968, 3 March 1969 and 4 March 1970. Her length had increased to 109 at the second capture and 111 and 118 at the third and fourth respectively. She must have been at least one year old at the time of her first capture and hence was more than three years old at her last capture. A male marked while probably still in his first month of life had records spanning 28 months and at his last capture he was of adult size but not especially large. The fact that two of these 24 basilisks recaptured spanned more than two years with their records indicates that their longevity is relatively great compared with most small lizards in the tropics.

Spatial relationships. Hirth (1963a) found that *B. vittatus* of all ages and both sexes regularly occupy small home ranges from a minimum of 7.9 m^2 to a maximum of 19.8 m^2. The home ranges in his study were polygons plotted on the basis of 13 to 16 recaptures. Ranges were found to average a little smaller for males than for females, and a little smaller for adults than for young. "Mature basilisks . . . have a strong attachment for a certain region within their home range. This is usually a pile of coconuts, which serves as both a basking and a feeding site."

In my study, 29 movements were recorded after an interval of a month or more. The longest distance was 152 m, and shifts of 79, 62, 43, 43, 41, 37, and 37 m were also recorded, but most movements were in the range 4.6 m to 23 m. These records suggest considerably more mobility than found by Hirth, and probably reflect alterations or shifts of home range over periods of months, as available cover and other habitat features are altered by flood and drought, tide, or human activity.

Temperature relationships. Hirth (1963a) obtained body temperatures of 476 juveniles and 242 adults. In both groups 35 was the preferendum, with progressively fewer records for each half-degree up to a maximum of 38.5 (with just one record). The lowest body temperature was 23.5. Substrate temperature was most often about 32.5 and air temperature about 29.5. Hence, usually a body temperature was several degrees warmer than either the air or the substrate, emphasizing the heliothermic tendencies of this basilisk. Hirth indicated the following thermal thresholds for *B. vittatus:* minimum voluntary tolerance 23.5 to 26.5; basking range 26.1 to 33.0; normal activity range 33.1 to 37.5; ecological optimum 35.3

(±.05) for juveniles and 34.7 (±.07) for adults; maximum voluntary tolerance 36.6 to 38.5; critical maximum 41.0 to 44.6; lethal 41.0 to 47.0.

Reproductive cycle. At Portéte there were obviously gravid females in the series captured in October 1967 and March, May, June, August and September 1968 but several captured in January 1968 and 1969 did not appear gravid. In both January samples there were hatchlings (from eggs laid in October?) and larger numbers of older young as well as adults. In March samples there were no hatchlings. The 15-16 March 1968 and 4-6 March 1970 samples contained second- and third-month young, but the 1-3 March 1969 sample contained only those in their 3rd month (minimum 63 mm) and larger. In all three March samples there were many young in the 70-85 mm size range, three to five months old, hatched October to December from eggs that were laid mostly in August and September. A sample from 6-9 May 1968 had a group of hatchlings (presumably from eggs laid in late February) and many large young 68-101 mm, about three months old or older, but no young of intermediate sizes. A three-month pause in breeding extending over part of November through January and part of February is indicated. A sample for 11-14 June parallels the early May sample, except that both the principal groups of young have made further growth. The hatchling group has not only newly emerged young but others of various sizes up to 55 mm, perhaps five or six weeks old. The previous crop of young, now at least four months old have minimum lengths of 76. Samples from 29-31 Aug. 1969 and 2-4 Sept. 1968 have hatchlings and older young of graded sizes, indicating continuous reproduction throughout the spring and summer months. The 28-30 Oct. 1967 sample is notable in having a high proportion of young, representing all sizes from hatchlings up to adolescents, and indicating a high level of reproductive activity continuous for many months previously.

In summary, the combined evidence, from reproductive state of adult females and from occurrence of young of various sizes, indicates a breeding season beginning in mid-February or a little earlier and continuing through October. In November egg-laying is greatly reduced and it remains at a low level through December and January (Fig. 8).

An adult female captured and marked on 6 May 1968 was judged to be gravid but was not much distended. Probably she had ovarian follicles that were still not mature and these may have been destined for her second clutch, as there is much egg-laying in February and March. The same female was shot on 4 Sept. and then contained uterine eggs nearly ready for laying. An output of four clutches per breeding season seems a reasonable estimate but on the conservative side.

The data concerning growth indicate that females mature in time to conceive approximately a year from the time of their own conception. Those conceived toward the end of one breeding season might contribute one small clutch of eggs at the end of the next breeding season, or they might postpone reproduction until the third breeding season. For example, a female of 46 mm was caught and marked on 23 Jan. 1968, when probably still in her first month of life, and was recaptured on 16 March, 14 June and 4 Sept. 1968. She made typical growth, and on 4 Sept. had attained the minimum size of sexual maturity (86 mm) and had enlarging ovarian follicles (2.5 mm) that might have matured by the end of October.

At Tortuguero, Hirth (1963a) found juveniles to be present during every month of his study—June through September and January through April—but they were most numerous in August and September.

Probably the Tortuguero population conforms with the seasonal trend that I found at Portéte, but Hirth was not on hand to observe the October to December build-up to the maximum numbers of juveniles and he did not specifically mention the scarcity or absence of hatchlings in March and April.

In 12 instances the number of unlaid eggs was determined in Portéte females by palpation of captured animals that were almost ready to lay, or by dissection, and in every instance there were 2, 3 or 4 eggs, $\bar{x}=3.17\pm.20$. In nine females from southern México (KU) clutches were larger, with from 3 to 5 eggs, $\bar{x}=4.10$. Hirth (1963a) found an average of 4.2 eggs in 25 females at Tortuguero. I found clutches of 3, 5 and 6 eggs in females at Barro Colorado in the northeastern corner of Costa Rica. For the 49 clutches combined the average is 3.90, range 2 to 6.

Ctenosaura similis (Gray)

Description. Large, stocky, body flattened with stout, moderately long limbs and tail (more than twice length in hatchlings but less than twice in adults), scalation on body fine and granular, on tail in whorls that are relatively coarse and spiny; a crest of erect, spinelike middorsal scales on body; a gular pouch and transverse gular fold; color dull black with pale tan patches in adults, bright green with dark markings in small juveniles, tan with dark reticulations in hatchlings.

Range and habitat. This ctenosaur occurs from the Isthmus of Tehuantepec on both coasts in southern México south to Panamá on the Pacific versant. It is abundant chiefly in low, hot areas having a pronounced dry season. In Costa Rica it extends onto the Meseta Central nearly to Alajuela, 900 m.

The preferred habitat is open woodland or savanna. Hollows in limbs, tree trunks or fence posts, or burrows beneath tree roots, old buildings or rock piles provide shelter.

General habits. C. similis is both terrestrial and arboreal, largely herbivorous but also predatory. The hatchlings are strikingly different from adults in behavior as well as appearance. At first strictly terrestrial, they are much more slender and agile than the adults and are alert and active; small insects are their main food (Montanucci, 1968). There is gradual transition to the relatively bulky, phlegmatic, partly arboreal, largely herbivorous adult. The adult browses rather indiscriminately on tender herbaceous vegetation, but also preys on various small vertebrates and large insects.

A hatchling, when followed, will run from one clump of vegetation to another, increasing the length and speed of its dashes if it is hard pressed, but not relying on any regular refuge for escape. While still less than a month old, it becomes somewhat scansorial, perching on tree trunks, fence posts, or boulders, climbing to escape in times of danger and returning to regular retreats for periods of inactivity.

The adults are strongly attached to their retreats and use elevated perches nearby, ducking into shelter at any disturbance. Adults are much shyer than young. At times they will scurry for shelter when a person is as much as 65 m away, especially when surprised in an open situation such as a beach or cultivated field. However, one that is near shelter may allow a person to pass within a few meters without moving. At Finca Taboga many inhabited hollow fence posts and would habitually bask on top of the posts, ready to scuttle into the cavity at any alarm. Elsewhere, hollow trees, logs or boulders provide basking places that have secure shelters within or beneath them. Often the retreat is a burrow in the ground probably excavated or enlarged by the lizard. Taylor (1956:182) stated: "Often a

large tree, especially if there is a hollow trunk or hollow limbs, offers shelter to a colony of ten or more of these large lizards. From here they may forage a hundred yards or more in varying directions." Doubtless this species is territorial as is *C. pectinata* studied by Evans (1951), but where several or many live crowded in close proximity there are likely dominant and subordinate individuals. Judging from the homeward dashes of flushed individuals, forays of "a hundred yards" are possible but are relatively rare, and the usual foraging radius is much shorter. The recapture records of first-year young indicate that these lizards are confined to remarkably small home ranges.

Growth. For 8 recaptured, gains in length were 65 to 74 in 36 days, 72 to 84 in 33, 70 to 78 in 33, 70 to 78 in 31, 73 to 84 in 31, 76 to 99 in 45, 86 to 143 in 228, and 95 to 170 in 162. All these growth periods were in the rainy season. The last two records listed are especially significant because they span relatively long intervals. The last one listed grew at almost twice the rate of the one just before it. Thus a wide range of individual variation in growth is indicated. Table 5 shows the trend of growth into the third year based on recognizable size groups of young; measurements or estimates of length were made on substantial series. Age-size correlation for an individual making typical growth is suggested in Table 3.

By the time the young are a year old they have more than tripled in length, and are approximately half the length of adults. By the following winter they have become sexually mature but are still much smaller than average adult size. The clutch is large and variable with great increase from first to second clutches and especially to those of large adults. The fact that hatching extends over several weeks in any one locality suggests the possibility that a female may produce a second clutch. Because of the high productivity, young sometimes appear in great abundance in places where the adults are not especially in evidence.

Spatial relationships. In 16 instances I recorded distances between captures for first-year young recaptured several weeks after they were originally marked. The 4 longest movements were respectively 131, 55, 49 and 46 m; the remaining 12 were all in the range 4 to 16 m and averaged 10.4.

Temperature relationships. Ctenosaurs are limited to warm climates and are heliothermic. The 54 body temperatures obtained, all from juveniles (Fig. 12), indicate a preferendum between 36 and 37. Ctenosaurs were caught most often at air temperatures between 29 and 31, and their body temperatures were from four to eight degrees above air temperatures. Doubtless temperature relationships are similar in adult ctenosaurs, except that their relatively bulky bodies change more slowly than those of the young in response to environmental change. Ctenosaurs spend much of their time basking in sunshine, even when temperature is relatively high. Absorption of heat may be reduced by position and orientation; for instance, one perched on a fence post may have only its head exposed to sunshine, absorbing relatively little heat in the warmer part of the day.

Reproductive cycle. C. similis proved to have the most restricted breeding season of any of the lizard species studied (Fig. 18). Hatching is limited to a period of weeks from late April to June. Incubation is mainly within the dry season. At Boca de Barranca on 9 Feb. 1970 a female of 212 mm was found to contain 21 oviducal eggs 24 x 18 mm and probably almost ready to be laid. This female was of a size typical for ctenosaurs late in their second year. At El Salto, Escuintla Province, Guatemala, a female of 262 mm on 17 Feb. 1971 contained 34 oviducal eggs each about

30 x 19 mm. Adult females dissected at Finca Taboga 18 March 1965 (2), Playas del Coco March 1965 (1) and Finca Pacifica (15 km NNE Finca Taboga) 25 May 1968 (1) all had enlarged oviducts but minute ova and obviously had completed their egg-laying for the season.

Alvarez del Toro (1960:93) stated the incubation period to be 90 days. Perhaps it is somewhat less in many instances. Most egg-laying must occur in December and January with some in November and February. At Tilarán, 562 m, 30 km NE Finca Taboga, in a cooler and wetter climate than that usually inhabited, young estimated to be 120, 110 and 110 mm were seen on 25 December 1967. They were smaller than any of the numerous young seen at low altitudes in the same week and seemed to be retarded by at least two months compared with these young. Presumably the cumulative effects of decreased insolation and lower temperature delayed the breeding season, extended incubation, and slowed the growth of the hatchlings to bring about the differences observed. At Quepos, also, in December 1967 and January 1968, young were observed to be relatively small as compared with those in Guanacaste, and nearly as much retarded as those at Tilarán. However, newly emerged hatchlings were found at Quepos on 1 May 1968, somewhat earlier than they appeared in Guanacaste. Retardation of young at Quepos presumably was the result of persistent overcast and relatively low insolation during the summer and autumn months of high precipitation, re-

Table 5. Lengths* of young *Ctenosaura similis* showing the trend of growth.

	Guanacaste highways no. 1 and 21	Playas del Coco and Sardinal	Finca Taboga† and Boca de Barranca	Quepos
First year				
early March				60 (in one)
early May				69 (65-78 in 5)**
late May		59.4 (56-63 in 24)**	70.7 (57-82 in 48)†**	
late June				77.4 (60-90 in 21)
early July		71.2 (63-97 in 24)**	83.8 (63-107 in 52)†**	
mid-Aug.	91.5 (77-110 in 42)			
late Aug.				85.0 (70-105 in 20)
late Nov.			135 (110-175 in 25)	
late Dec.	151 (120-190 in 28)		129.5 (120-140 in 10)†	
Feb.	165 (150-180 in 6)	143 (115-180 in 15)**	149 (120-170 in 10)	
Second year				
April			162 (130-190 in 40)	
May	168 (140-190 in 6)**		162.3 (110-200 in 26)	138 (125-150 in 3)
July	166 (130-190 in 16)	196 (177-220 in 4)**		
Aug.	171.5 (143-216 in 34)			163 (160-170 in 3)
Nov.			211 (190-220 in 16)	
Dec.	217 (200-250 in 19)			
Feb.	211 (190-240 in 8)		205 (180-240 in 13)	
Third year				
April			222 (190-280 in 30)	
May	225 (200-260 in 8)		230 (210-290 in 18)	
July	245 (200-290 in 12)			

* Means, extremes and numbers in samples.

** Measured (other records are estimates).

† Finca Taboga; other series in column 4 represent Boca de Barranca.

ducing the time available for feeding and other activities.

Iguana iguana (Linnaeus)

Description. Giant iguanid, having a middorsal crest from nape onto tail, consisting of a series of greatly enlarged, sickle-shaped scales; crest longest at middle of neck, tapering abruptly anteriorly but very gradually posteriorly on body and tail; head short, with large, prominent eye, with a large circular scale at angle of jaw which exceeds both ear and eye in diameter; a pendulous nonextensible dewlap (more prominent in male) bordered posteriorly by a transverse fold, and having a midventral series of much enlarged, flattened, denticulate scales anteriorly; tail somewhat compressed, attenuate and whiplike, 2 to 2.5 times length; scales fine and granular, tending to form regular transverse and longitudinal rows on body, limbs and tail; color predominantly green, but with series of several sometimes obscure, wavy black transverse bands on body and tail; in old males ochraceous or orange suffusion tends to replace green of dorsal surface.

Range and habitat. Humid tropical lowlands from Sinaloa and Veracruz through southern México, Central America and into South America. The habitat is in forest and forest edge, especially along streams.

General habits. Iguanas climb rapidly and easily; in tall trees they appear to be secure and at ease even in the presence of humans or natural enemies. These herbivores find much of their food in trees and take tender foliage, flowers and fruits of many kinds, but the diet includes some animal food, especially in young. Iguanas have an affinity for water, and this is especially noticeable where the species occurs in a relatively dry climate. There the population is concentrated along streams and rivers. The lizards enter the water readily, and swim well. Usually they submerge while swimming, and with leisurely movements of the long flattened tail, progress rather rapidly through the water. Much time is spent in trees over the water. Characteristic behavior of one that is approached while in a tree too small to provide security is to plunge into the stream and swim beneath the surface to a protected spot beneath an overhanging bank, behind exposed tree roots, or in dense vegetation. Iguanas may swim far from shore, in rivers or even in the ocean. They have some gregarious tendencies; many of both sexes and various sizes may congregate in a single tree where there is an attractive food supply, and many females may gather in a small area for egg-laying (Rand, 1968).

Reproductive cycle. Although the iguana occurs mainly in warm moist climates that have relatively little seasonal change, there seems to be a well defined annual breeding season, most females laying their eggs within a period of weeks, and young appearing in large numbers at about the same time each year. In Chiapas, southern México, breeding occurs from October to December and eggs are laid in March or April according to Alvarez del Toro (1960:89). However, Neill and Allen (1959) found hatchlings in April in British Honduras. At Tortuguero in northeastern Costa Rica, Hirth (1963b) found that egg-laying occurs in the March-April dry season, and hatching coincides with the arrival of the summer rainy season. Hatchlings have been found emerging on 6 June. At Barro Colorado in the Panama Canal Zone, Rand (1968) found a relatively advanced breeding schedule. From the end of January to the first week of March an estimated 150 to 200 gravid females swam across a narrow channel and deposited their eggs on an open area of an islet. Hatching was concentrated in the last weeks of April or the first week of May,

coinciding with the onset of the rainy season.

The following observations made in the course of my study, in western Costa Rica, indicate concentration of egg-laying there in January and February.

28 Dec. 1967, Sardinal: Female of 410 mm contained 17 follicles 28 mm in diameter.

17-18 Jan. 1968, Quepos: Egg-laying seemingly at a peak; groups of people hunting iguanas with dogs and carrying gravid females captured when they came to the ground to deposit their eggs.

11 Feb. 1970, La Irma: Females noted excavating nest burrows at several places along streambank; group of 4 flushed from their unfinished burrows within space of 9 m.

15 Feb. 1970, Playas del Coco: Female distended with eggs flushed from gully.

17 Feb. 1970, Finca Taboga: Nesting in progress with many open burrows in sandbanks; as many as 4 females flushed simultaneously from burrow areas.

The presence of young of different sizes in a single sample suggests an extended breeding season, but variation in hatchling size and different growth rates complicate reconstruction of the breeding cycle. The sizes of 8 juveniles from my study areas at Playas del Coco and Boca de Barranca suggest hatching as early as mid-December or as late as early May. Twenty-two juveniles (KU) from scattered localities in Costa Rica and southwestern Nicaragua had a mean length of 78±1.17 (70-87). Presumably their average age was a little more than a month, and their hatching must have been concentrated in early May from eggs laid in late February or early March.

The protracted period of egg-laying raises the possibility of multiple clutches, but is is not known whether a female occasionally or regularly produces more than one clutch in a season. Another unsolved problem is the time required to attain sexual maturity. At Finca Taboga in April 1968, when many iguanas could be observed simultaneously climbing in the same large tree, there were at least three size groups distinguishable: 1) adults more than 300 mm (usually more than 400) in length, 2) young about half the length of the adults, 160-170 mm, and 3) young about one-fourth the length of the adults, 75-90 mm. Possibly some iguanas breed when they are two years old, but it would not be surprising if normally more than two years were required to reach maturity.

Sceloporus malachiticus Cope

Description. Medium-sized, coarse-scaled, with scales heavily keeled and spine-tipped; tail about equal to length in young, a little longer in adults; color greenish tan with nine or ten pairs of dark dorsal spots in juvenile and adult female, yellow-green with no well defined dorsal pattern in male; ventral surface with paired longitudinal deep blue areas separated by black medially; female and young have smaller and paler blue areas and lack the medial black.

Range and habitat. S. malachiticus occurs from Honduras and El Salvador into Panamá. In Costa Rica it is absent from low elevations, but occurs over a wide altitudinal range from about 650 m up to more than 3000 m.

Its habitat is in relatively open, sunny situations, such as woodland edge and clearings, fence lines having live trees (some with cavities), and logs, woodpiles, gardens, rough-barked trees, rock walls, tile roofs of buildings, pasture and meadowland where there are occasional boulders or outcrops and thorny bushes for shelter. The species occurs over a wide

range of climatic conditions, from high montane cloud forests to xeric forests of scrubby and thorny type.

General habits. Like other members of its genus *S. malachiticus* is a heliotherm; the basking habit is especially noticeable where the species occurs in relatively cool climates. A characteristic location for basking is the top of a boulder or fence post. In such situations the lizards are conspicuous and may be seen from a distance. As the day becomes warmer, they leave their basking spots and move to the shaded side of the post or boulder, usually with head directed downward, prepared to make a rush to the ground to catch any prey that passes. The lizards are shy, may take alarm at a person 15 m or more away, and cannot be easily stalked. One that is approached moves toward shelter and if further disturbed it will scramble into a secure place of concealment, beneath a boulder, into a rock crevice, or into a decaying stump or log, or in a cavity of a limb. The dash to shelter is usually only a few meters at most, indicating that home ranges are small, but over a period of weeks a lizard may shift from one tree or rock outcrop to another, abandoning temporarily at least the site of its earlier activities. Young are more terrestrial than adults, are less shy, and less adept at escaping and finding adequate shelter. A juvenile that is flushed may run from a boulder and seek concealment in a tuft of grass or beneath a pebble where it can be easily caught.

Food consists of insects and arachnids. A litter of young born in confinement ate termites avidly but was relatively indifferent to other small insects of similar size. As in other species of *Sceloporus*, ants probably figure prominently in the diet.

Growth. Because the extreme wariness of the lizards intensified with stalking and capture, recaptures of marked individuals were few. For 2 recaptured males gains in length were 36 to 38 in 14 days and 44 to 56 in 53. For 7 recaptured females gains in length were 33 to 64 in 167 days, 35 to 36 in 14, 40 to 43 in 14, 40 to 44 in 19, 46 to 48 in 14, 44 to 48 in 92, and 48 to 64 in 105. Except for the last one listed, all these growth periods were mostly or entirely within the dry season. For the entire group growth averaged 4.6 mm per month, but with much difference between individuals. A sample of five young on 10 Dec. 1967, soon after birth, averaged 31.7 mm, and 139 days later on 28 April, another sample of 11 presumably born at the same time averaged 53.6 mm. Thus here normal growth averaged at least 5 mm per month for several months. Sexual maturity is attained by females still far short of average adult size, and growth continues through and beyond the first year of life. A female measured (48mm) and marked on 28 April and recaptured on 11 Aug. appeared to be gravid on the latter date and was approximately the minimum size (64 mm) of sexual maturity. Age-size correlation is suggested in Table 3.

Spatial relationships. Of 8 recaptured lizards, 2 (both young females) were recovered at the original location after 13 days and 19 days. Others had moved distances of 1.2, 1.5, 3.0, 4.6, 9.1 and 21 m in intervals of 14 to 105 days.

A typical home range seems to encompass only a few square meters and is located with reference to a secure shelter, with an adjacent elevated perch for basking. The home range, or at least its central area, is defended as a territory. An adult male and female are often found in close association, but members of the same sex are well spaced. As a result of this spacing, territorial encounters between adults have not been observed but young of various sizes have been seen to display toward others and chase them.

Temperature relationships. Eighty body temperatures were obtained. Two lizards

that were inactive (beneath a log and in a hollow stump) had temperatures of 15.7 and 20.8 respectively. All others were active and their temperatures ranged from 20 to 36 but were concentrated in the range between 34 and 35. As shown in Figure 15 the lizards usually maintain body temperatures from 7 to 15 degrees above air temperature while active. By persistent basking they are often able to maintain sufficiently high body temperatures to be active even when environmental temperatures are much below the preferred level. They are able to initiate activities at body temperatures somewhat below 20 and under favorable conditions may then rapidly raise the body temperature by basking. At air temperatures of 16.2 (4 p.m. 19 April 1968) and 16.0 (ca. 9 a.m. 22 April 1968) lizards were found active, with body temperatures of 31.5 and 32.6 respectively.

Reproductive cycle. Viviparity in *S. malachiticus* is seemingly correlated with its occurrence at medium to high altitudes. The gestation period has not been recorded, but is believed to be as much as four months. Perhaps it is considerably longer at the highest altitudes where the lizards occur. Viviparity limits the frequency of reproduction, and perhaps the number of young per brood. Plate III (lower) illustrates relative sizes of a female and her newborn young.

Marion and Sexton (1971) discussed the reproductive cycle of *S. malachiticus* as revealed by 10 collections averaging about 10 individuals each, obtained in central Costa Rica at various times of the year. Most adult females from mid-January to early April contained only non-yolked follicles. Yolked follicles were found only in late June (July, August and September were missing from the records), and embryos were present in most of those examined from early October to late January. The authors concluded that growth of ovarian follicles occurs through June, July and August and ovulation occurs in early September. Males seemed to be in breeding condition (testes at maximum size and an abundance of mature sperm in the epididymes) only in June. In March and April testes were undergoing progressive enlargement and some had mature sperm, but sperm was not yet present in the epididymes.

My data from the Cartago study area correspond fairly well with the annual cycle described by Marion and Sexton. Population samples in late 1967 and 1968 showed the following trends.

1 Nov.	Only adults and subadults present; most females obviously gravid.
10 Dec.	Newborn young and some large enough to be nearly a month old present along with adults; larger young absent.
14 and 21 Jan.	Young from newborn size up to 40 mm make up a large part of the population, which otherwise consists of adults.
6 March	Young, from those recently born up to 52 mm make up the greater part of the population.
22 and 28 April and 5 May	Population has a high proportion of partly grown young with dividing line between young and adults no longer sharply defined.
6 and 16 June	Population consists mainly of large young and adolescents.
11 Aug.	Recently matured adults and large young make up most of population.
1 Sept.	Population consists essentially of adults, with a few well-grown young.

In an earlier study of the reproduction of *S. malachiticus* in Costa Rica (Fitch 1970:45) I suggested the possibility that females might produce more than one litter annually because, in a pooled sample representing various localities and altitudes, there were young indicating occurrence of births at almost all times of year. Samples from high altitudes, especially, do not conform well with the seasonal trends postulated by Marion and Sexton and shown by my records from Cartago. Table 6 shows the occurrences of gravid females and young in five series totaling 89 specimens collected at high altitudes. The first two series show that there are many births in December, January and February. The remaining three series (KU) were collected at the opposite time of year and show that at high altitudes there are also many births in May through August—perhaps as many as in the winter months.

Under the climatic regime of Cartago sexual maturity is attained within six months of birth. One female caught and marked soon after birth (33 mm) on 1 Jan. had grown to 64 mm on 16 June, and another perhaps born in early February and marked on 28 April (48 mm) was gravid when recaptured 11 Aug. (length 64). Both were typical of their population in growth and probably produced young late in their first year of life.

At higher altitudes activity is limited by low air temperature, clouds and mist, and both gestation and growth must be retarded. As a result, attainment of maturity is probably delayed, and young born in February might not produce their own litters until the second summer at an age of around 18 months. The 36 young from high altitudes in the February, July and August collections seem to represent births in the months January, February, and April through August. On 24 Oct. 1967 near Vara Blanca, 1800 m, a juvenile of about 40 mm was seen, probably representing an August birth. The evidence strongly suggests that at high altitudes births occur throughout the year, with partial or complete breakdown of the seasonal schedule prevailing at lower elevations because individuals are unable to mature in time to produce litters at the age of one year. In general, montane lizards are longer lived than their lowland relatives,

TABLE 6. Seasonal occurrence of gravid females and recently born young in *Sceloporus malachiticus* from high altitudes.

				Young	
Locality	Date	Number in sample	Gravid females lengths	Length	Estimated age in months
Río Cotón and R. Coto Brus, 1500-1800 m	mid-Feb. 1965	26	60, 61, 65, 68 70, 72, 75, 76, 79 83, 90	28, 30, 30, 31, 33 38, 39, 41 48	< 1 1.5 2.5
Volcán Barba, 2100 m	10-21 Feb. 1965	9	70, 73	31, 33 39, 41	< 1 1.5
Volcán Irazú, 2900-3100 m	3-5 July 1947	15	63, 64, 66 70, 74	32, 35 40, 40, 44 48	< 1 2 2.5
Volcán Barba	11-17 July 1951	11	69 76	31	< 1
Volcán Barba, 1860 m; and Cerro de la Muerte	9-10 Aug. 1951	28	68, 70, 71	33, 35, 35, 36, 36, 37, 38 41, 42, 43, 44, 45, 45, 48	0.5-1.5 1.5-2.5

and have lower reproductive potentials (Stebbins and Robinson, 1946; Fitch, 1972). The effect of altitude on reproductive effort (including time required to reach maturity, number of young in litter, frequency of litters and size of young at birth) needs to be studied in *S. malachiticus*.

Sceloporus squamosus Bocourt

Description. Small, with fine keeled scales; limbs relatively short, body slender, tail attenuate (more than twice length); head reddish brown, dorsal coloration brown with pale dorsolateral stripes; ventral coloration dull white, with no trace of bright display colors characteristic of most other members of the genus, in males at least; sexes essentially alike in size, coloration and markings (Plate III, upper).

Range and habitat. Occurs from Chiapas southeast at low and moderate elevations to northwestern Costa Rica on Pacific versant, and extends into dry valleys of Caribbean versant in Guatemala and Honduras. The lizards are mainly terrestrial, sometimes climbing on boulders, low bushes, or the bases of trees. The habitat is in relatively open situations where vegetation is sparse and there are intervening patches of bare ground.

General habits. Only a dozen of these lizards were seen in the course of my field work in Costa Rica. They were found at Playas del Coco, Sardinal, near Liberia (28 km east northeast of Sardinal) and at two intermediate localities. All were in open, disturbed situations, such as nearly barren fields grazed by horses and cattle, or roads or trails. The lizards were not wary. When flushed they ran only a meter or two at a time, and were captured with relative ease compared with *S. variabilis* and especially *S. malachiticus*.

Sceloporus variabilis Wiegmann

Description. Medium small, stout-bodied, having fine keeled and mucronate scales; tail usually 1.3-1.5 times length; color dorsally tan with dark brown blotches (about 12 pairs from nape to base of tail), each blotch having a smaller, whitish area on its posterior side; blotches continue onto tail where they tend to form chevrons (proximally) or faint rings (distally); dark dorsal blotches obscure or indiscernible in adult males but with their whitish posterior portions emphasized, and a pair of dull whitish dorsolateral stripes developed; sides darker than dorsum; dark spot on each shoulder, sometimes obscure, limbs and toes with faint dark bars; large, paired ventral patches of bright blue and rose in adult males (faint in immature males, absent in females and hatchlings); pair of large indented and well differentiated postanal scales in males; 7 to 12 femoral pores. (See Plate III, middle.)

Range and habitat. Occurs from Tamaulipas in northeastern México south into Central America, mainly at low and intermediate altitudes, chiefly on the Pacific slope, to Puntarenas in Costa Rica. In Costa Rica it is limited to the relatively dry northwest.

Its habitat consists of dry, open ground with wood such as rough barked trees, logs, fence posts, or driftwood providing shelter and objects to climb upon. Sandy beaches with abundant driftwood and the dune groves adjacent to such beaches provide the best habitat and support the densest populations. Farther inland it is found in gullies and washes in rocky places, and on steep slopes—situations where ground vegetation is sparse.

General habits. S. variabilis maintains a high body temperature and spends much of its time basking. It does not emerge in the morning until sunshine has warmed its nighttime retreat, and upon emerging it moves into the open, finds a well insulated object such as a dry piece of wood against which to flatten itself to receive the

maximum solar radiation, and basks to raise the body temperature to the preferred level before beginning feeding, territorial activities or courtship. Compared with *S. malachiticus* it is less scansorial and spends a high proportion of its time on the ground.

Compared with other common species of the genus, *S. variabilis* is intermediate in degree of wariness. Depending on the situation and the individual, flushing distance of one approached by a person is usually between 3 and 6 m but may be less. One that is flushed does not seek shelter immediately but retreats to a more secure place. It may move only a few centimeters downward and to the opposite side of a fence post, or it may make a dash of 10 to 15 m to a clump of brush. If further pursued or disturbed, the lizard attempts to escape in any of several ways. Most frequently it enters a cavity or crevice in a tree trunk or fence post or it may climb high into a tree, even out onto small twigs; or it may suddenly burrow into the substrate of soft soil or sand with brisk lateral wriggling movements, then lie inert and fairly well concealed, even though the tail and top of the back may protrude. The burrowing usually occurs under the shelter of a grass clump or other screening vegetation, after the lizard has darted away from its pursuer, and the ruse is used especially in sandy situations where there are no better hiding places. The food consists of small insects and other arthropods.

Growth. A total of 285 records of growth were obtained from marked individuals. For 10 of those recaptured that were considered representative, gains in length were 25 to 40 to 47 to 55 in 75, 42 and 51 days; 25 to 35 to 43 to 48 to 53 to 54 in 75, 42, 51, 55 and 44; 25 to 36 to 44 to 50 to 54 in 96, 61, 42, and 47; 26 to 58 in 147; 27 to 59 in 173; 29 to 52 to 58 to 60 in 94, 98 and 32; 25 to 37 to 52 in 45 and 49; 28 to 44 to 57 in 93 and 55; 28 to 41 to 59 in 54 and 97; and 26 to 53 in 120. In this list the last two were males, all others were females.

For the first three months mean growth rate is approximately 5.5 mm per month; it slows to 4.4 mm per month in males and 2.9 mm per month in females for the second three-month period. Females may grow to minimum adult size in as little as four months from the time of hatching. Males grow a little faster at least in the later stages, and attain larger adult size (Table 3).

Spatial relationships. Figure 11 summarizes distances between captures after an average interval of several months in a large sample of *S. variabilis*. During the course of field work with these lizards I often learned to recognize individuals because of pecularities in their size or pattern or regenerated tail or because they were distinctly marked with paint. Typically, such individuals were seen time after time at the same station, and they obviously had an attachment for objects providing shelter. One that was stalked or chased sometimes made an escape dash or a series of dashes taking it as much as 24 m from the starting point, but usually the distance was much less. Normally, the lizard remained within a radius of a few meters, but it might temporarily shift its activities to outlying points where shelter was adequate, or might alternate between several points. Figure 11 shows that short movements—up to about 15 m—are most numerous, with 14% between 15 and 25 m and only a few exceeding 25 m. However, the maximum recorded movement was 690 m, and five lizards exceeded 600 m. How such long shifts may come about in a lizard ordinarily of such sedentary habits was demonstrated at Boca de Barranca when a spring tide occurred in the late afternoon of 14 April 1968. As piles of beach wrack were inundated, lizards ran confusedly in search of shelter or swam

frantically as they were swept away by the current. Massive piles of wrack were momentarily lifted, shifted and then allowed to resettle in a new position as each wave advanced and receded.

The recurring hazard to which beach lizards are subject was mollified in this instance by the fact that it took place in daylight and was not accompanied by high wind or rain. Other more devastating spring tides that were not actually witnessed took place during the course of the study and changed the configuration of the beach and the distribution of wrack on which lizards depended for shelter. In storms lizards clinging to floating debris, especially those in cavities of hollow logs or stumps, might survive a long time and might be carried for distances much greater than the 0.69 km recorded in the present instance.

Temperature relationships. These lizards are heliophilic, and during periods of activity body temperature is typically three to five degrees above air temperature (Fig. 19). Upon emerging from nighttime shelter, the lizard is nearly always well below its preferendum, and it basks in an exposed place until body temperature is elevated. In the tropical climate where the lizards occur, keeping sufficiently cool is often the chief problem. Then insolation is avoided and the lizards seek insulated shelters, or stay in the shade, with much reduced activity, so that they are much more difficult to find. As shown in Figure 19, body temperatures varied from 27.5 to 39.5 but were concentrated in the range 31 to 35. A preferendum in this range is characteristic of the genus *Sceloporus* and has been noted in many of the other species (Bogert, 1949; Brattstrom, 1965). Air temperatures at the times of capture ranged from 26.0 to 34.6 but were concentrated between 28 and 30.

Reproductive cycle. In 18 clutches I

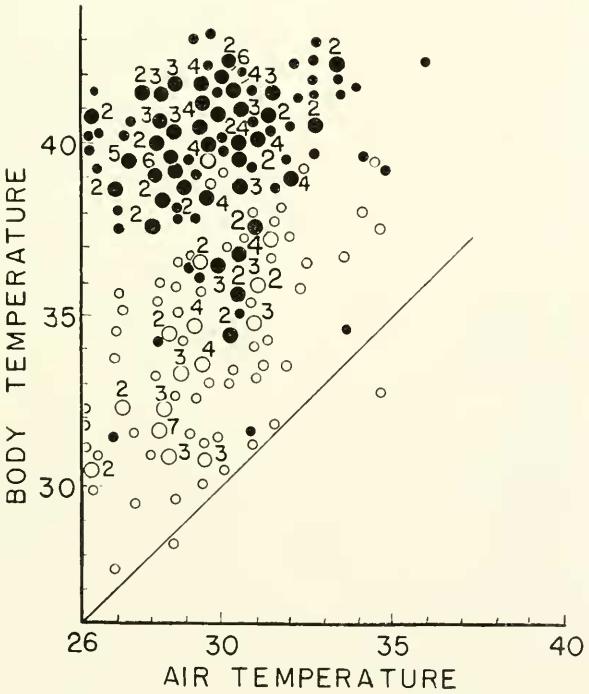

Fig. 19. Body temperatures and adjacent air temperatures of *Cnemidophorus deppii* (open circles) and *Sceloporus variabilis* (closed circles) from Playas del Coco and Boca de Barranca. Small and large circles show numbers as in Figure 10.

found an average of 3.0 eggs (1 to 5; Fitch, 1970:59). *S. variabilis* is thus one of the less prolific species of the genus, but living in the tropics in a climate that is mild throughout the year, it produces clutches frequently. Small young were found in each sample at both Boca de Barranca and Playas del Coco, but their numbers fluctuated greatly from one time of year to another indicating that productivity was at low ebb at some times and relatively high at others.

At Boca de Barranca, for instance, in November and December of 1967 a large sample was rather uniformly divided among lizards of many size groups, from hatchlings to large adults, showing that reproduction had been occurring at a high level for several months previously. However, in February young had become relatively scarce and in early April and the end of June the population consisted almost entirely of adults. In late August, both in 1968 and 1969, the population had a high proportion of hatchlings and few young of intermediate size, showing that a new period of increased reproductive activity was underway after a long period of relative quiescense. During most of January, February, March and April there were no gravid females, but some became gravid in May and from then through November a substantial portion of the females were gravid (Table 7). Hatching reached a high level in July and continued high through November, tapering off in December.

TABLE 7. Percentage of month-to-month samples of adult female *Sceloporus variabilis* that were gravid.

Season of sample	Boca de Barranca		Playas del Coco	
	N	% gravid	N	% gravid
Nov. 1967	6	16	12	0
Dec.-Jan. 1967-68	17	6	10	0
Feb.-March 1968	34	0	24	0
April 1968	31	0	....	....
May 1968	25	40	34	30
June-July 1968	28	29	37	16
Aug. 1968	20	55	11	45
Feb. 1969	34	24	15	33
Aug. 1969	26	42	19	53
Feb. 1970	23	13	18	17

TABLE 8. Months of hatching of *Sceloporus variabilis* extrapolated from sizes of young in each sample.

	Playas del Coco (N=236) % of year-round sample	*Boca de Barranca* (N=232) % of year-round sample
Jan.	3.0	1.7
Feb.	5.1	3.0
March	3.4	....
April	5.5	.9
May	.9	.4
June	1.8	3.5
July	11.0	12.9
Aug.	10.6	26.3
Sept.	14.0	17.3
Oct.	13.2	15.1
Nov.	22.4	15.1
Dec.	9.3	3.9
Total	100.0	100.0

The trends of seasonal cycles at Boca de Barranca and Playas del Coco are similar in most respects (Fig. 13), but the November-to-May lull in breeding is more complete at Boca de Barranca (Table 8).

Family **Anguidae**

This almost cosmopolitan family has few representatives in Costa Rica and is not prominent ecologically.

Gerrhonotus monticola Cope

Description. Medium-sized, elongate with short, pentadactyl limbs and heavy cylindrical tail; deep lateral fold with granular scales from behind ear to groin; dorsal body scales in 16 longitudinal rows, rhomboidal, keeled except in nuchal region; ventral scales smooth, in 12 longitudinal rows; in most females and in young dorsal color is pale brown with a series of middorsal black spots, sides darker

with occasional white flecks; adult males often heavily pigmented, mostly black, speckled with many light colored greenish-yellow flecks or spots which have some tendency to align themselves longitudinally in broken streaks along the body; ventral surface dull gray with dark pigment concentrated in the middle of each longitudinal scale row forming faint longitudinal lines.

Range and habitat. Occurs at high altitudes in Costa Rica from at least as far north as Volcán Poas southeastward through the Cordillera Central and Cordillera de Talamanca into Chiriquí in Panamá. Inhabits cloud forest, forest edge and sometimes brush or pastureland or vicinity of buildings, sheds, corrals, or rock piles. It is usually dependent on dead wood such as stumps or logs with loose bark, boards or woodpiles.

Reproductive cycle. A series of 38 (KU) from Volcán Irazú, Volcán Barba and Vara Blanca in July consists of three indistinct size groups: 1) juveniles 30, 36, 41 and 52 mm in length, judged to represent births in June, May, April and January, respectively; 2) 11 adolescents (including two gravid females) 58 to 65 mm in length and judged to be 8 to 10 months old; 3) 23 adults 68 to 86 mm in length, of which all ten females are gravid. Nine females have follicles 2 to 6 mm in diameter, and the two largest have uterine eggs recently ovulated. From analogy with the closely related *G. coeruleus,* similar in size and living at similar temperatures in the coastal region of the northwestern United States, it is suspected that gestation in *G. monticola* lasts from seven to ten weeks. A concentration of births in October and November could be expected from the females having enlarging follicles in July; most of these females would have required several weeks for their ova to mature before conception.

Three series of specimens (KU) from Cerro de la Muerte were studied. Sixteen in August included one recently born young, one female with nearly full term embryos, four nongravid females that may have given birth recently, one female with recently ovulated eggs and two with enlarged follicles. In this series the adolescents are poorly represented, and the adult females seem somewhat accelerated in the timing of their breeding compared with those discussed in the previous paragraph. A June sample has one female with large follicles, one with uterine eggs, and a 56 mm adolescent perhaps born in November. A February-March sample has two adult nongravid females, a 34 mm juvenile perhaps born in January, and a 55 mm adolescent perhaps born in August.

At Hacienda El Prado in November 1967, I captured a gravid female and a 46 mm juvenile, perhaps born in July.

The combined evidence from occurence of gravid females and of juveniles suggests that births are concentrated in October and November, but occur in smaller numbers throughout the remainder of the year. Females probably mature in time to produce first litters at an age of approximately one year.

Family Teiidae

This large family of the Neotropical region and southern North America is well represented in Costa Rica. Three species of *Ameiva* and one of *Cnemidophorus* were included in my study. These are medium-large, active, terrestrial lizards occurring in high population densities and playing an important role as predators on arthropods, as competitors of other insectivorous animals and as a food source for larger predators. *Ameiva* and *Cnemidophorus,* considered congeneric by some authorities, are somewhat different ecologically, *Ameiva* occurring in various types of forest and *Cnemidophorus* in more open, xeric situations. There is over-

lap. In many localities in northwestern Costa Rica, *A. undulata* and *C. deppii* occur in the same habitat and seem to be competitors for food and space, but on the average *C. deppii* is in more open situations. Potential competition is even greater between *C. deppii* and *A. quadrilineata,* which often are beach lizards, remarkably similar in habits and habitat. *A. quadrilineata* occurs as far north as Quepos and *C. deppii* as far south as Boca de Barranca, but it has not been determined whether their ranges meet or how the transition occurs in the 90 km interval between Barranca and Quepos. At Portéte, *A. quadrilineata* and *A. festiva* occurred together, but the latter was much scarcer and much more closely limited to dense vegetation. At Quepos both *A. quadrilineata* and its near relative *A. undulata* were present, but the latter was confined to leaf litter and undergrowth in forests and plantations.

Ameiva festiva (Lichtenstein)

Description. Large, stout, with long, pointed snout, moderately long tail, and powerful legs; scales are fine and granular on dorsum and sides, but on ventral surface are large, smooth plates, in eight rows (six anteriorly); tail with enlarged, heavily keeled, spiny scales in regular whorls; color dark brown with a pale (yellow or greenish or bluish) middorsal narrow stripe extending from the tip of the snout posteriorly along the body and tail, where it becomes obscure, irregular with indented margin on body; a pair of broad lateral black stripes on body; one or more dorsolateral series of cream-colored, bluish-tinted, irregularly shaped spots and streaks between pale dorsal stripe and black lateral stripe, or encroaching on the latter; ventral surface dull white or with reddish or greenish suffusion of throat in male; tail bright blue in hatchling, gradually fading to brown in older lizards.

Range and habitat. Occurs from México at the Isthmus of Tehuantepec south and east through Central America, and in Colombia, South America, chiefly in humid tropical lowlands; absent from northwestern quarter of Costa Rica, where there is a pronounced dry season, but present on Pacific slope in humid southwest *(A. f. occidentalis);* occurs to at least 600 m in subtropical zone (Turrialba). It is primarily a forest lizard, but requires basking places with sunshine, and it thrives in seral situations such as provided by plantations of banana or cacao. It is present on the coast in coconut plantations, and on the beach, but in these places it is much less numerous than *A. quadrilineata* and tends to stay in or near cover such as hedges or thickets.

General habits. A. festiva is a highly mobile terrestrial lizard, which maintains a high body temperature by basking, and travels with rapid jerky movements, finding arthropod prey by visual, tactile and olfactory sense, with almost constant probing or digging while active. Yet it spends a relatively large part of its time inactive under shelter. Even when weather conditions are optimum, the lizards emerge late in the morning and retire early in the afternoon. When the sky is overcast or rain is falling, they do not emerge. At Pandora, Smith (1968) noted that throughout rainy periods, often lasting for a week or more, they kept to their shelters and were not seen in the banana groves.

Even when actively foraging, these lizards spend long periods within a few square meters, moving around the same log or pile of debris. After being chased into cover, one might be found after a few minutes back at the original location. A home range is probably comparable to one of *A. quadrilineata,* or even smaller.

Growth. Only one record of growth was obtained; a female at Portéte marked 9 May 1968, when she was 69 mm in

length, was recaptured on 12 June, grown to 81 mm, and gravid. Such rapid gain indicates that *A. festiva* grows and matures at least as fast as *A. undulata* and *A. quadrilineata*, and most individuals probably reach sexual maturity between three and six months after hatching.

A puzzling aspect of Smith's (1968) findings concerns the small average and maximum sizes that he indicated. In his 1963 sample of 225, he stated that males ranged from 39 to 100 mm ($\bar{x}$=67.6) and females from 37 to 94 ($\bar{x}$=70.0). Many adults of both sexes that I examined exceeded 100 mm. Two gravid females that I collected at Pandora on 11 March 1965 had lengths of 82 and 104.

Reproductive cycle. Smith (1968) concluded that there was no seasonal variation, since all mature females, regardless of the month they were collected, contained yolked follicles or oviducal eggs and/or corpora lutea. However, the 81 gravid females that he recorded were chiefly from late July, August and early September, and evidently the samples from other months were small. From experimental females, Smith determined that the interval between the initiation of deuteroplasmic activity in a set of follicles and their ovulation is approximately eight weeks, and egg-laying occurs after another three weeks or a little less. Hence a total of nearly three months is required for production of a clutch. Smith estimated that a female would produce an average of at least three clutches annually. In this he was conservative, as there is ample time for production of four clutches if the 11-week period for production of a clutch, and the lack of any pause between successive clutches as Smith observed, are accepted as the rule.

A sample of 91 *A. festiva* (KU) from a dozen Costa Rica localities but mostly from Los Diamantes, Turrialba, Suretka and Tenorio, were collected in March (7), July (31), August (31) and September (22). For these 4 months gravid females made up 29, 19, 13 and 32% of the samples, respectively; young in their first month made up 43, 16, 16 and 23%, and supposed second-month young made up 0, 19, 10 and 9%. Supposed third-month young made up 6% in July and 19% in August. Arbitrary age estimates were made as follows: first month, 41 to 55 mm, second month, 57 to 69 mm, third month, 70 to 80 mm. Sight records of 50 from Portéte are as follows: January (6): hatchlings 33%, second-month young 17%; March (8): hatchlings 25%, second-month young 37%; May-June (6): hatchlings 16%, second-month young 16%, third-month young 50%; late August-early September (26): hatchlings 15%, second-month young 8%; October (4): all large young and adults. The trend of the records tends to bear out Smith's contention that there is year-round breeding but the samples are too small to show significant differences between months.

Ameiva quadrilineata (Hallowell)

Description. Stout-bodied, similar in most respects to *A. undulata* but markedly smaller; distinctive in having a broad black, dorsolateral stripe on each side; brown middorsal area has pale lateral edges where it contacts black dorsolateral stripes; this dark stripe is bordered below by a narrow white stripe extending from temple to groin; below the white stripe sides are spotted with white; throat yellowish in male. There is only one loreal on each side. Sexual difference in size is slight. Pattern remains distinct in adults but it is more sharply defined in the juvenile, which has a bright blue tail.

Range and habitat. Humid lowlands of Costa Rica on both coasts. On the Pacific Coast it extends north only slightly beyond Quepos. On the Atlantic it occurs from Nicaragua to Panamá. It extends

far inland (Suretka, Limón Province and San Isidro del General, San José Province) in humid forest but also is a typical beach lizard and in both the localities where I observed it the species was limited to beaches and nearby areas. Although in both areas its population density was high on the beach, it did not seem to extend much more than 100 m inland. At Tortuguero, Hirth (1963a) found *A. quadrilineata* in all zones of the strand, but most abundant in open sunny areas under coconut trees.

At Portéte I observed these lizards mainly in a coconut grove, where there were broken patches of sunlight and abundant shelter including jagged coral rock, logs and sticks, dried palm leaves, piles of coconut husks, and in places a dense mat of ground vegetation. At Quepos the lizards were far more abundant and were found over a wider range of habitats. They were found even on the open sandy beach where there was no growing vegetation but where tidal wrack provided abundant shelter. They were most numerous in coconut groves, but were present also in plantations of bananas and other arborescent crops, and often retreated into the tangled vegetation at the edge of a mangrove swamp on the leeward side of the front dune.

General habits. As a heliotherm *A. quadrilineata* requires sunshine and open areas. Its usual habitat is much more open than that of its near relative, *A. undulata*, and it is less shy and secretive. With slow and cautious movements an observer can often approach within a meter or two. However, it cannot be easily herded or driven like the more active *Cnemidophorus deppii*. An attempt to catch one in this way nearly always resulted in the lizard becoming increasingly wary and finally hiding in a burrow or beneath some object. If routed from such shelter, it would immediately scramble to a new hiding place.

These lizards travel with brisk, jerky movements and obtain their prey by active search. Much time is spent in digging and probing, and seemingly much of the prey is found by olfaction. In the stomachs of 244 *A. quadrilineata* that Hirth (1963a) examined at Tortuguero, talitrid amphipods, tenebrionid beetles and lycosid spiders were by far the most important foods.

When active, *A. quadrilineata* has the high body temperature and high metabolism characertistic of teiids, but it spends relatively little time in activity above ground, emerging only after the sun has warmed the soil and air, and sometimes retiring again to shelter about midday. In the rainy season, in cloudy or inclement weather, it may not emerge at all for periods of days. At Tortuguero, Hirth found population densities of 12 to 26 per acre with adults generally more abundant than juveniles.

Growth. From 32 recaptures, Hirth (1963a) found that beyond 40 mm males grow faster than females, with a slowing trend in both sexes. From his figures the correlation between age and size in Table 3 is tentatively suggested. The smallest female with oviducal eggs found by Hirth was only 48 mm and hence might have been only two months old, but most fecund females are probably more than four months old.

Spatial relationships. At Tortuguero, Hirth (1963a) found home ranges of the following average dimensions in square meters: adult male 445, adult female 188, juvenile male 269, juvenile female 227. He found that adult males roam more or less randomly throughout the home range, but adult females have strongly defined centers of activity, usually a favorite log. Juveniles have less strongly defined centers of activity. Hirth had less data for the dry season in March and April than for the

remainder of the year, but he found some indication that home range size was reduced in the dry season, because of high temperature of the sand surface inhibiting movement in open situations, and lack of the tidal debris that attracted the lizards at other times.

Turner, Jennrich and Weintraub (1969) suggested that home ranges plotted from minimum polygons are nearly always smaller than actual ranges, and they proposed a correction factor based upon the number of records used in plotting the area. Applying their correction factor to Hirth's figures, Turner *et al.* calculated an average home range of 1045 m^2 for adult males and 417 m^2 for adult females.

In my field work an impression of extremely small home ranges such as found by Hirth was gained from repeatedly observing what seemed to be the same individuals at approximately the same places. I did not notice the tendency for females to have more strongly defined centers of activity.

Temperature relationships. Hirth (1963a) obtained 698 body temperatures at Tortuguero, with corresponding air temperature and substrate temperature for each. The histogram from these records, arranged on a half-degree scale, showed a typical skewed curve with greatest frequency at 37.5 degrees. Hirth suggested the following thermal categories for *A. quadrilineata:* ecological optimum, 37.6 (± .06); normal activity range, 34.6-40.0; basking range, 27.6-34.5; minimum voluntary tolerance, 24.0-27.5; critical maximum, 45.1 (± .17). Hirth's histogram shows that activity is greatest when air temperatures are in the neighborhood of 29 to 30, and 32.5 seemed to be the optimum substrate temperature. The lizards maintain their temperatures within their preferred range by active movements—to heated sand and sunlit places when body temperature is too low and to shaded damp places or beneath objects when body temperature is too high.

Reproductive cycle. Hirth (1963a) stated that at Tortuguero "During the mating season, the flanks of most males become greenish-blue . . ." His field observations were made during the period of June to September in two different years, but he believed that the peak of egg-laying was in May and June, and young were present in greatest numbers in August and September. However, young were present also in June, July, and January through April, and according to the reports of some residents of the area, they were present year-round.

At Pandora, about 30 km south of the site of my study at Limón and 110 km southeast of Tortuguero, Smith (1968) found that all mature females, regardless of the month they were collected, contained yolked follicles, or oviducal eggs and/or corporea lutea. He therefore concluded that they were reproductively active throughout the year, but most of the lizards were collected between 15 July and 11 Sept. Relatively few were collected at two-week intervals between 1 Oct. 1965 and 31 May 1966. Smith's field work was done in banana plantations, and he emphasized the homogeneous nature of the cover and the heavy year-round rainfall.

My observations were made chiefly at Quepos, in a hotter and sometimes drier climate than at Pandora or Tortuguero. Nevertheless, at each sampling there seemed to be some gravid females, and there were always hatchlings or young near hatchling size. For specific dates the percentage of the population consisting of young estimated to be less than a month old were as follows: 14 Dec. 1967—22; 17 Jan. 1968—37; 24 Feb. 1970—13; 7 March 1969—24; 1 May 1968—10; 20 June 1968—7; 21 Aug. 1968—22; 25 Aug. 1969—7. The high percentage of young in mid-January seems to indicate peak production of eggs

in late October, with other high points indicated in mid-December, early May and late September (Fig. 9). October corresponds with the peak of the rainy season, and it seems that in general a high level of egg-laying is correlated with heavy precipitation. Nevertheless, production continues at somewhat depressed levels through the dry season.

Ameiva undulata (Wiegmann)

Description. Medium-sized, heavy-bodied, long-toed, long-nosed, long-tailed, with fine, granular scales dorsally on the body, and large scales on the ventral surface and tail; color dull, predominantly tan, with black marks on the sides (Plate IV, upper); salmon-colored suffusion on chin, throat and chest in breeding males; young longitudinally striped on body, with blue tails.

Range and habitat. A. undulata has 12 recognized subspecies, with a range that extends from southern México, on both coasts, south through Guanacaste Province of northwestern Costa Rica, and as far as Quepos, Puntarenas Province, on the southern coast. It occurs mainly in lowlands, but in Costa Rica encroaches onto the Meseta Central as far as the western outskirts of San José.

The habitat is leaf litter in open type of woodland, or woodland edge, or situations near to woodland. In the course of my field work these lizards were found in xeric scrub and brush, in lowland swamp forest, gravelly edges of streams, in cafetal, banana groves, pineapple plantations, fields, pastures, along railroad tracks and roads, and in suburban yards and vacant lots.

General habits. A. undulata is a strictly terrestrial lizard which finds its prey by active search, guided by visual, tactile and olfactory sense. It moves about with a quick, jerky gait, digging, probing and nosing in niches, holes and crevices for arthropod prey including pupae and eggs. In the course of its normal activities the lizard changes direction frequently so that in travelling only a few meters it crosses its own trail several times without progressing much farther from the starting point, and without venturing far from a potential refuge.

The lizards are heliotherms that maintain extraordinarily high body temperatures and are active only when the sun is shining or has been shining recently. Even at the times of year when they are most active the lizards spend only a few hours a day above ground and remain concealed and quiescent most of the time. At some times of year adults are not in evidence and perhaps spend periods of days or weeks inactive without emerging.

One that is followed tends to keep near a hiding place except when it makes an occasional dash across open ground from one thicket or log to another. One that is active may be readily approached to a distance of 3 m or even 2 m by a person moving slowly and cautiously. The lizard may even move up to or in contact with the feet of a person standing in the vicinity, but any sudden movement will send it scurrying for shelter. If an observer moves cautiously following the lizard, the latter continues its activities but tends to maintain or increase the distance between it and the person, and to keep a barrier such as a log or bush between. At any further alarm it makes a short and rapid dash for shelter, and hides beneath a log, in a burrow or merely beneath the leaf litter. If there is no further disturbance, the lizard may emerge slowly and cautiously after a long pause to look about warily with only its head protruding. Having emerged from shelter, the lizard may lie quietly, watching, while a person moves about in the vicinity. A lizard that has escaped into leaf litter may move beneath the leaves

and emerge a meter or more from the spot where it took shelter.

Growth. Twenty-nine marked *A. undulata* were recaptured a total of 49 times after periods of weeks or months and in every instance there was some growth. For 11 that are considered most representative, gains in length were 41 to 62 to 89 in 52 and 91 days, 50 to 57 in 14, 50 to 67 in 39, 52 to 85 in 99, 63 to 86 in 85, 65 to 86 in 35, 67 to 88 in 102, 69 to 98 in 148, 70 to 90 in 85, 70 to 89 in 144, and 74 to 96 in 104. The last individual was a male. Sex was not determined in the second and third; all others were females. The records of the first individual listed are especially significant in showing growth from the size of a hatchling to that of an adult in 143 days. For 3 young in the length range 40-60 mm gain per month was 12.0 mm, for 4 in the range 61-70 gain per month was 8.6, for 11 in the range 71-80 gain per month was 6.7 and for 15 in the range 81-100 gain per month was 5.8.

Spatial relationships. For the individuals recaptured the intervals between successive records averaged 39 days, and most movements were less than 20 m (Fig. 11), with 18% in the range 20-40 m. Stalking and catching the lizards often involved prolonged following and maneuvering, and the area covered during such a pursuit bore out the impression that home ranges with radii of approximately 12 m are typical. Adult males and females and young were much alike in their behavior, and in the extent of areas covered.

Temperature relationships. Activity is normally concentrated between 9 a.m. and noon. Body temperatures ranged from 29.6 to 40.5 (Fig. 17), but only one was below 33 and a third of the total were in the range 34-35, lower than in some other species of ameiva which live in more open habitat, (Fitch 1968). Most captures were made at air temperatures between 28 and 31.

Reproductive cycle. Percentages of adult females from Guanacaste that were gravid in different months were as follows: 42.9 of 7 in February, none of 4 in March, 31.5 of 13 in May, 63.5 of 11 in July, and 57.1 of 7 in August. The ratios of young to adults varied greatly in different seasonal samples. On 24 Dec. 1967, 20 km NE Finca Taboga, young of 45-50 mm, presumably between one and two months old, were abundant, but no other sizes could be found. On 18-19 March 1965 at Finca Taboga many young of 45-65 mm, probably from one to 2.5 months old, were seen, but no adults. Thus samples from December through March usually had a high proportion of immatures and few or sometimes no adults. However, the largest sample, obtained on 3 Feb. 1970 at Las Pavas, contained 72 lizards, with many adults and young of all sizes. The samples from April, May, July, August and September all contained a high proportion of adults including gravid females. Seemingly reproduction is at its lowest ebb in the early spring dry season, but is at its height immediately afterward, in April and May and the ensuing months, resulting in the production of a large crop of young about midsummer. Meanwhile the adult females continue to produce successive clutches of eggs at intervals of a few weeks, with the result that the total population and the proportion of young continues to increase until late fall. Reproduction is more inhibited by the dry season in the lowlands at La Irma (Fig. 18) than in the more equable climate of the Meseta Central at Las Pavas (Fig. 9).

At Sardinal a female of 79 mm contained three eggs, and a female of 87 mm contained two. Both were probably first clutches. Nine gravid females (KU) from the Yucatán Peninsula contained two to seven unlaid eggs. For the combined sample of 11 clutches, $\bar{x}=4.8$.

Cnemidophorus deppii Wiegmann

Description. Slender, medium-sized, long-tailed (more than twice length), long-nosed, long-toed, with fine granular scales dorsally on the body, large flat scales in 6 to 8 rows on ventral surface of body, and large keeled scales on tail; large scutes on anterior parts of fore- and hind-limbs, which have granular scales posteriorly; color predominantly brown dorsally with 7 thin longitudinal stripes, and dull white ventrally; in adult males dorsal surface is suffused with pale green on anterior parts, and ventral surface anteriorly is suffused with deep blue; tail bright blue in young, fading to gray in adult. (See Plate IV, upper middle.)

Range and habitat. C. deppii occurs on both coasts of México (northern Veracruz and Michoacán) southward into Honduras on the Atlantic slope and to southern Costa Rica between Puntarenas and Quepos on the Pacific slope.

In Costa Rica this species is prominent as a beach lizard. It occurs from the coast a few miles inland, but is found in greatest numbers in sandy situations with sparse vegetation, especially dunes of the ocean front. It often forages in beach wrack of the intertidal zone but is more at home on the upper beach where there are clumps of grass and patches of sea grape. Farther back from the beach it frequents groves, open woodland, scrub, and plantations, mainly in level sandy situations.

General habits. This is a terrestrial, diurnal lizard, the most active and agile of all the species studied, and gives an impression of haste and urgency as it moves about in a devious course, poking, probing and scratching for its arthropod prey. Correlated with this intensive activity is the lizard's high metabolism and maintenance of high body temperature, near 40. The lizards are active chiefly at times when the sun in shining. Emergence from nighttime shelter is noticeably later than in other lizards such as *Sceloporus variabilis* in the same areas. While temperatures are relatively low and sunshine is not intense, the lizards spend much of their time in sunlight, but as temperatures rise, they retreat to shaded situations and activity rapidly wanes during the heat of the day. Beyond midday few are active in the places where they were numerous during the morning hours. Hatchlings and other young sometimes continue their activity after adults have retired underground.

Like other species of racerunners that have been studied, these have remarkably small home ranges that can be traversed in an almost instantaneous dash. In addition to some open ground, each home range includes one or several shelters such as a log with holes inside or beneath, a trash pile, a thick bush, or a patch of low dense vegetation. At any suspicion of danger the lizard will move toward such a shelter, sometimes continuing to forage with no show of alarm. Seeming confident of its own speed and elusiveness, one may merely move away ahead of an approaching person, maintaining a separation of a few yards. If the person moves between the lizard and the nearest escape covert, the lizard often will change direction and cut back sharply with a sudden dash to reach the edge of the shelter, where it resumes more leisurely behavior. If cut off from such retreat it will make a longer dash to an alternative covert in a distant part of the home range. On the areas where the lizards were hunted, burrows of land crabs were numerous. A lizard that was cut off from shelter and hard pressed had only to duck into a burrow to escape. Sometimes a lizard made a long dash directly toward and into a crab burrow suggesting that the place was a habitual and well remembered refuge. On other occasions pursued and tiring lizards made rapid erratic searching movements over the ground surface for a second or more

before finding a burrow which may have been remembered inexactly or may have been located by chance. A lizard closely pursued or cut off from its intended shelter often changed direction with a sudden dodge and stopped with confusing suddenness, sometimes concealing itself beneath the ground surface or beneath a small object such as a stick or dried leaf.

Growth. A total of 124 marked racerunners were recaptured from one to four times after substantial intervals. Selected records for 13 that are considered representative follow. For 5 recaptured males, gains in length were 36 to 70 in 95 days; 41 to 74 in 92; 30 to 42 to 50 to 72 in 20, 55 and 94; 35 to 72 in 202; and 46 to 78 in 117. For 8 recaptured females, gains in length were 32 to 76 in 173 days; 39 to 77 in 154; 35 to 51 in 172; 35 to 61 in 167; 38 to 46 to 59 in 34 and 59; 34 to 46 to 54 in 128 and 49; 35 to 54 in 149; and 32 to 55 in 148. Most of these were marked while still in their first month and recaptured after growing to adult or adolescent size. They indicate that adult size may be attained in as little as four months but usually five to seven months are required. Males grow faster than females and are mature when they reach 70 mm; females are mature at a minimum length of 58 (Table 3).

Spatial relationships. Linear distances between capture sites were measured for 181 racerunners recaptured after several weeks or several months (Fig. 11). The distances ranged from 0 to 170 m but only 5 exceeded 60 m. In view of the ease and rapidity with which *Cnemidophorus* travels, most of the distances were remarkably small. Most were in the range 3 to 24 m (Fig. 11), with abrupt reduction in numbers for greater distances.

The short distances shifted by most individuals that were recaptured even after several months suggest that home ranges have some stability in time. At the Playas del Coco no. 1 study area, numerous juveniles were captured and marked in November and December 1967, but in the dry season few of them could be found and racerunners seemed to have become much scarcer. With the arrival of another rainy season, in May and June, racerunners were again much in evidence. Those present included many marked as juveniles in late autumn, but grown to adult size in the interval. These were consistently near their original capture sites, strongly suggesting that they had continued to live in their original ranges but perhaps with much reduced activity or actual dormancy for extended periods during the dry season.

Temperature relationships. A total of 189 body temperatures of active racerunners were obtained of which most were in the range between 39 and 42—higher than in any of the other lizard species studied, but within the range known to be characteristic of this genus in the Temperate Zone (Bogert, 1949; Fitch, 1956; Brattstrom, 1965). The active lizards had temperatures from 29.1 to 43.2 (Fig. 19). More were captured at air temperatures between 29 and 30 than in any other one-degree range, and numbers tapered off rapidly at higher and lower temperatures. Thus in the active lizards, body temperatures 9 to 12 degrees above air temperatures were typical (Fig. 19). The lowest air temperature at which an active racerunner was found was 26.1. At much lower air temperatures the lizards are too inactive to emerge and bask. The threshold of activity is therefore unusually high in this species. At the Boca de Barranca and Playas del Coco study areas racerunners emerged in the morning notably later than did other lizards such as *Sceloporus variabilis.* Greatest activity occurs at about midmorning, and by mid-afternoon it has virtually ceased.

Reproductive cycle. Noteworthy differences are evident in the seasonal trends

between the populations at Playas del Coco and at Boca de Barranca. The breeding season is much more restricted at Playas del Coco. There, in February 1968, 1969 and 1970, the population consisted mainly of adults and large young. In 1968 there were no hatchlings but in 1969 and 1970 hatchlings and other small young were well represented. In late March 1968 a sample of 34 had only one hatchling and five larger young. A late May 1968 sample of 119 had mostly adults but with one first-month young and four that were probably in their third month. Adult females were mostly gravid. A July 1968 sample of 89 consisted essentially of large adults, the females gravid, but there were two partly grown young. An early August 1968 sample of 107 had four hatchlings but otherwise consisted of adults and adolescents. A late August 1968 sample of 128 consisted mostly of adults and adolescents, but had 15 small young and three of intermediate size. A sample of 160 from the end of November and the first two days of December 1967 consisted mostly of young of all sizes with only three adults. A late December 1967 sample was similar, and both had many hatchlings. These samples show that egg-laying begins in the latter part of May, reaches a high level in June and remains high through October, then tapers off rapidly in November and December. Through the dry season, December to April inclusive, egg-laying is at low ebb but occurs occasionally, so that some hatchlings may be found at all times of year (Fig. 18). The July and August samples indicate a pause of about five months in reproduction.

At Boca de Barranca there is little or no reduction in the rate of egg-laying during the dry season. Samples from early January (51), early February (133), mid-February (99), late February (120), early April (211) and late May (105) all had many hatchlings and other young. Samples from late June to early July (89), and late August (191) had especially high ratios of hatchlings and juveniles. In all these population samples, the proportion of young less than three months old ranged from 17.6 to 50.5%. Hatchlings were least well represented in mid-November and early January samples, indicating some slackening of reproduction in September and October—the late rainy season.

There were obviously gravid females in each sample from both localities. In May through August samples the majority were gravid and obviously reproduction was at a high level at this time of year. In a series (KU) from Managua, Nicaragua (175 km NNW Playas del Coco) in late May and early June 1956, there were 11 females 60 mm or more in length, and all of them were gravid.

Eight of the females that were captured and marked at Playas del Coco and Boca de Barranca when they were noticeably distended with eggs were recaptured in gravid condition after intervals sufficiently long for them to have deposited the first clutch, 33, 34, 34, 35, 48, 49, 51 and 51 days. The female recaptured after a 35-day interval was less distended at the second capture than at the first, as was one of the females recaptured after 51 days. Eight others captured in nongravid condition appeared gravid when recaptured, after intervals of 34, 35, 41, 43, 50, 51, 54 and 58 days; three that were gravid at an early capture appeared nongravid after intervals of 34, 45 and 56 days. The female recaptured when nongravid after 34 days was unusually distended with eggs and obviously was nearly ready to produce a clutch at the time of her first capture, and she may have produced a second clutch before she was captured again. Obviously the intervals between successive clutches are somewhat variable. From the records cited above, and from analogy with the better known *C. sexlineatus* (Fitch, 1970:

97), I suspect that an interval of approximately 25 days may be typical.

Six clutches of eggs of *C. deppii* average 2.8, varying from one to four according to the size of the female. Females produce their first small clutches of eggs at 5 or 6 months, when they are still far short of average adult size and are growing rapidly. A female productive throughout the breeding season might produce about 17 eggs at Playas del Coco and somewhat more at Boca de Barranca if clutches are produced at approximately monthly intervals. Actually, neither the interval between clutches nor the incubation period are known, but perhaps both approximate those of the somewhat similar *C. sexlineatus* in the United States in which the interval between clutches is sometimes as little as three weeks, and incubation has been variously reported as 53 days in Oklahoma (Carpenter, 1960), 60 days in northern Kansas (Fitch, 1958a) and 61 days in North Carolina (Brown, 1956). In southern California, Bostic (1966) obtained evidence of a 50-55 day incubation in *C. hyperythrus*.

Family Scincidae

This cosmopolitan family is represented by few species in Costa Rica. *Scincella cherriei* is a small, abundant, oviparous, insect-eating species, usually in leaf litter of forests or plantations, and widely distributed in lowland areas in wet climates. *Mabuya mabouya* and *M. brachypoda* are medium-sized active, partly arboreal, viviparous lizards. They occur in relatively low population densities and have relatively low reproductive potentials.

Mabuya brachypoda Taylor

Description. Elongate, slender, similar to *M. mabouya* in most respects; limbs short, failing to meet when adpressed, separated by a wide gap; dorsum brown, almost uniform, with or without traces of dorsolateral stripes; a dark band on each side; scales usually in 30 (sometimes 28 or 32) longitudinal rows.

Range and habitat. Occurs from southern Guerrero south through the Pacific coastal region of southern México and Central America to southeastern Costa Rica. Its habitat requirements are similar to those of *M. mabouya* but it occurs in drier places.

Reproductive cycle. Two museum specimens (KU) from Boca de Barranca, 26 July and 21 Aug., each had 4 embryos about 18 mm in length. One from Tenorio, about 700 m elevation, on 21 Aug. had 4 small embryos. Webb (1958) and Davis and Dixon (1961) mentioned a total of 14 females in Michoacán and Guerrero, southern México, that had embryos in June or July, or produced litters in one of these months.

Mabuya mabouya (Lacépède)

Description. Medium-sized, slender, elongate, having small hexagonal polished scales usually in 26 to 30 longitudinal rows; a transparent disc in lower eyelid; limbs well developed, overlapping when adpressed; brown dorsally, with scattered black spots or dots and whitish markings, with a pair of narrow, cream-colored dorsolateral stripes and a similar pair of ventrolateral stripes and a wider dark area between.

Range and habitat. A remarkably widespread species occurring from Veracruz and Sinaloa in México south through Central America and the Amazon Basin in South America and on many West Indian islands including the lesser Antilles. In Costa Rica it occurs in both Caribbean and Pacific lowlands, and to altitudes of at least 800 m. Populations of the two versants are noticeably different; those of the Caribbean have frontonasal and rostral scales in contact, fewer (26-28) body scale rows, and better developed body stripes.

Taylor (1956) considered the two to be distinct species.

Although confined to hot climates, these skinks occur in a variety of habitats, both natural and disturbed—in rain forest, xeric woodland, banana plantations, coconut groves, rail fences, rock walls, and bridge abutments.

General habits. These skinks are secretive and wary; always found near shelter such as a hollow tree, crevice or burrow into which they escape at the slightest alarm, they are difficult to noose or catch by hand, and their population densities are usually low. Therefore, they are poorly represented in collections. They are largely terrestrial, but often are found on logs and tree trunks, and they climb well.

Like most other members of the genus, *M. mabouya* is viviparous. In this case viviparity is not associated with a cold climate, as it is with the other viviparous Costa Rican lizards studied—*Sceloporus malachiticus* and *Gerrhonotus monticola*. In the situations frequented by the skinks, eggs would usually be laid in burrows in shaded sites and so their incubation temperatures would be relatively low. Gravid females have the basking habit well developed.

Reproductive cycle. Fifty museum specimens (KU) were all collected in July and August. They consist of two poorly defined size groups—adults from 70 to 86 mm in length, and partly grown young. Ten of the twelve adult females are nonreproductive, but one from San Isidro del General on 22 Aug. has two follicles 3 mm in diameter, and one from La Lola on 10 Aug. has two nearly full-term embryos. Young make up about half the total sample and include specimens of 44, 49 and 50 mm, but 20 are concentrated in the narrow range 52 to 63 mm and might have all been born about the same time of year.

At Portéte on 4 March 1969 I captured a female distended with large embryos, and at Pandora on 11 March 1965 I captured one that had a single full-term embryo. These two records suggest that births may be concentrated in March. The lack of small young among the museum specimens collected in July and August, and the high proportion among them of young somewhat more than half-grown, sizes that might be reached at an age of four or five months, support this idea. It is tentatively concluded that in Costa Rica births are concentrated in March, but with some at the opposite time of year and perhaps throughout the entire year. The growth rate implied by this schedule indicates that young mature and conceive in time to produce litters when they are one year old.

Scincella cherriei (Cope)

Description. Small, elongate, bronze-colored with shiny scales, a long, heavy tail, and small pentadactyl limbs, the adpressed forelimb and hind limb overlap widely in juveniles and slightly in most adult males, but do not meet in large adult females; there are 30 or 32 scale rows around the body and 62 to 69 scales from occiput to vent; an irregular dark stripe behind eye extends along neck, obscure posteriorly; sides darker, dotted with black and tan, ventral surface yellowish, undersurface of tail gray, lower eyelid with transparent disc in center.

Range and habitat. S. cherriei occurs throughout much of Central America, from Tabasco, México, to Panamá, with four subspecies. In general it is limited to lowlands or intermediate elevations, and to humid climates. It is abundant in the eastern lowlands of Costa Rica, but relatively uncommon on the Pacific slope and perhaps absent from extensive areas of arid climate in Guanacaste in the northwestern part of the country.

The habitat is the forest floor of tropical rain forest, and forest edge, and in a

variety of disturbed situations. Many of those seen in this study were in cacao groves. Others were in low grassy and herbaceous vegetation in open woodland or scattered groves. Leaf litter is the most frequent shelter.

General habits. These skinks are furtive and secretive, usually remaining under cover. They sometimes emerge for brief periods of basking, but with part of the body or tail still concealed beneath a leaf or stem. Much of their activity takes place beneath the concealment of low vegetation or leaf litter; seemingly the food is found largely by olfaction. The lizards are strictly diurnal and limit their activity to relatively brief periods when humidity is high and temperature is moderate. Especially in midday heat of sunny weather, they are inactive, and in the cool of the morning do not show themselves until sunlight warms their hiding places. At any alarm the skink darts out of sight into a hole or crevice or beneath debris or surface litter. If the hiding place is superficial, trampling or turning of objects may cause the skink to show itself a second time in a dash for more secure shelter. Hiding places seem to be numerous and the escaping skink disappears after a dash of at most a meter or two.

Growth. For 12 recaptured, gains in length, all within the period 12 Nov. 1967 to 8 May 1968, were 25 to 31 in 77 days, 36 to 51 in 117, 35 to 52 in 177, 37 to 43 to 47 in 75 and 41, 43 to 51 in 77, 47 to 51 in 81, 48 to 53 in 116, 48 to 53 in 82, 49 to 54 in 77, 51 to 58 in 78, 52 to 57 in 117, and 53.5 to 56 in 117. It is noteworthy that each one recaptured had made substantial gain in length, although some were already in the size range of adults when they were marked. The tentative age-length correlation in Table 3 is based in part upon extrapolation from Brooks' (1967) growth curve for *S. laterale* showing the most rapid growth in the first month of life, since all the marked young of *S. cherriei* that I recaptured were more than a month old at the time of marking.

Spatial relationships. A total of 46 were recaptured after an average interval of 54 days. The longest movements (40, 38, 36.5, 35, 30, 27 and 27 m) were all made by females and, even excluding these records, the average distance for 23 females, 10.6 m, was a little larger than the average for 17 males, 9.7 m, indicating that females are the more vagile. Nearly half the recorded movements were in the range 6 to 12 m, and relatively few exceeded 21 m (Fig. 11), indicating that the usual home range is within an area of this diameter.

Temperature relationships. Body temperatures of these skinks were recorded from 22.5 to 31.0 with records especially concentrated in the range 25-27 (Fig. 14). For a tropical lizard this skink has a low temperature preferendum, but its body temperatures resemble those of the North American skinks that have been studied most *(Eumeces fasciatus, Scincella laterale)*. Body temperature tended to be the same as air temperature or only a little higher, thus these skinks are not heliotherms. Occasionally they have been observed basking in sunshine, but usually only briefly and with only part of the body exposed. Most captures were made in the range between 23 and 27 of air temperature. Ground skinks were found throughout the hours of daylight, but with definite peaks at mid-morning and mid-afternoon.

Reproductive cycle. Trends in reproductive status of the skinks at the Turrialba study area are shown by the following sequence of visits from November 1967 to February 1969.

12-16 Nov.: Sample of 50 included juveniles in first month (1), second month (2), and third month (3), and 21 adult females, only one of which was judged to be gravid on

the basis of external appearance. Three others dissected had only minute ovarian follicles.

28-29 Jan.: Sample of 47 included juveniles in second month (1) and third month (1), and 20 adult females of which 6 were judged to be possibly gravid.

8-10 Mar.: Sample of 65 included no small juveniles and one of third-month size (perhaps from an egg laid in November), and 34 adult females, most judged to be gravid; two of these were dissected and one had large uterine eggs and the other had medium-small (3 mm diameter) ovarian follicles.

20 Apr.: Sample of 32 included no juveniles less than three months old and consisted mostly of adults of which 14 were females. At least four of these were nearly ready to lay and shelled ova were discernible through the body wall.

8 May.: Sample of 22 included second-month young (3) and third-month young (2), and seven adult females of which four were judged gravid and one of these had uterine eggs visible through the body wall; another of the four dissected had recently ovulated eggs.

13 Aug.: Sample of 24 had first-month (1), second-month (3) and third-month juveniles, and eight adult females, all but one of which appeared gravid. Two that were dissected had medium large ovarian follicles (3 mm and 4 mm in diameter).

20-21 Feb.: Sample of 24 had only adults; a large number escaped, and all these were adults too. Of the 13 females, two had undeveloped gonads and 11 had ovarian follicles, mostly in early stages of growth, but up to a maximum diameter of 7 mm.

Although most of the Turrialba samples were small, they indicate seasonal change in the level of reproductive activity (Fig. 8). In November a breeding season is ending, most females do not contain developing eggs and the population has a high proportion of young from adolescent size down to hatchlings. In December through March, egg-laying and hatching rarely occur, and young hatched in November or earlier have been growing rapidly, so that the smaller size classes are not represented. Follicle growth is occurring gradually in adult females and some are many weeks ahead of others. Egg-laying becomes frequent in late March and young are becoming numerous by the end of April. Reproduction continues at a high level into early November, with females producing several successive clutches of eggs. Ovarian follicles develop slowly, since females recaptured over periods of weeks in March, April and May become more distended, seemingly from the same clutches of eggs. Young from eggs laid early in the breeding season would scarcely have time to reach mature size before the end of the breeding season; therefore, it may be inferred that one generation per year is the rule.

At Puerto Viejo, 71 km northwest of Turrialba, in the Caribbean lowlands, a series of 20 skinks was collected on 5 March 1965. These included hatchlings, older young of various sizes and five adult females, of which two had uterine eggs almost ready to be laid and the other three had large ovarian follicles. Obviously the halt in breeding in winter and spring indicated at Turrialba did not apply to this population living in a warmer and much wetter climate.

Greene (1969) examined 90 *S. cherriei* mostly from Costa Rica and found 16 gravid females, all from the months of March, May, June, July and August. Data concerning size of clutch (based on ovar-

ian follicles or uterine eggs) are available for 33 females including the 16 reported upon by Greene (1969) and 17 from Turrialba, Puerto Viejo and Beverly. Two each had one egg, 19 had two eggs and 12 had three eggs; $\bar{x}=2.33$. The size of the clutch tended to parallel size of the female.

DISCUSSION AND CONCLUSIONS

Every one of the many species and local populations studied had its own distinctive seasonal schedule and proved to be adapted in a somewhat different way from every other population to utilize the resources and avoid the rigors of specific environments. Although no two are just alike, there are several groups of species that are basically similar in their ecology.

The group that is probably the most different from all the others is that of the two giant iguanines, *Iguana iguana* and *Ctenosaura similis*. In addition to their large size these lizards have in common a largely herbivorous diet, relatively enormous clutches of eggs, with hatchlings that are remarkably small compared with the adults, a long period of growth, with sexual maturity postponed until late in the second year or even longer, and a breeding season extending over a small part of the year in the winter months. Typically oviposition occurs in the driest part of the year. As a result the incubating eggs receive maximum insolation. The young appear late in the dry season or early in the rainy season that follows it. The abundance of insects and of succulent vegetation in the early rainy season gives impetus to early growth. The timing of reproduction, though different from that of most other lizards in the same areas, is a logical one for areas having a pronounced dry season. However, *Iguana iguana* occurs also in regions that have consistently high precipitation and lack a marked dry season, and there is not much change in the timing of its reproduction. In rain forest and other situations of the Caribbean lowlands, where vegetation is dense, open areas of loose easily dug soil or sand for egg-laying may be of critical importance. Iguanas prefer riparian situations and often utilize open sandy banks or bars that may be submerged at flood stage. Timing of egg-laying so that eggs will be incubating during the driest part of the year is therefore of adaptive significance. In *Ctenosaura* the breeding season is more concentrated. The lizards live in relatively open situations, spend much of their time in burrows, and do much digging. Availability of nesting sites is probably less critical than in the iguana.

The largest group of species includes most of those that are characteristic of western Costa Rica in a climate characterized by a pronounced dry season—*Anolis cupreus, A. intermedius,* probably *A. biscutiger* and *A. sericeus, Cnemidophorus deppii, Ameiva undulata, Sceloporus variabilis* and probably *S. squamosus,* and *Gonatodes albogularis* in part of its range. All these are small or medium-sized species, insectivorous, oviparous and (except *Gonatodes*) heliothermic. They have a breeding season that extends through about half the year or somewhat more, including at least the months of May through October, the same individual producing eggs several or many times during this period. Then at the onset of the dry season or somewhat before it, reproduction declines to a low level or ceases entirely. For as much as half the year, November through May, there may be no reproduction. The population declines from its annual peak attained in late autumn. Meanwhile there is increase in average size. Some growth occurs in individuals of all size classes, and growth rates tend to be inversely proportional to the size of the individual. Consequently when the breeding season begins, the population consists of adults of various sizes, adolescents, and

immature lizards most of which are approaching adolescent size. As the breeding season progresses, there are steady increments to the breeding pool by newly maturing individuals until all or nearly all of the young from the previous season's crop have matured. Production reaches its annual peak at this stage. Meanwhile the first-laid eggs hatch and as hatchlings of this new crop begin to grow, they are replaced by successive increments of smaller ones. Eggs continue to hatch for several weeks after laying has ceased, and again the population builds up to an annual high point.

Two medium-sized, montane, viviparous insectivorous lizards, *Sceloporus malachiticus* and *Gerrhonotus monticola*, proved to have somewhat parallel trends in their annual schedules, and to differ from all other kinds. In both of them ovulations are concentrated in the June-August period, with births most frequent from early October to December. Reproductive activity thus is concentrated in the wettest and coolest part of the year. Young make most of their growth in the warmest and dryest part of the year and mature in time to produce litters of their own when they are about one year old. *S. malachiticus* conforms best to this schedule near the lower edge of its altitudinal range, as at Cartago in a relatively warm and dry climate. At higher elevation births are more evenly distributed through the year, and the lower temperatures retard gestation and growth, probably to the extent that an average generation extends over somewhat more than a year. In *G. monticola* also, there are some births throughout the year.

Two other viviparous lizards, *Mabuya mabouya* and *M. brachypoda*, differ from the above two species and each other in the timing of their reproduction. *M. mabouya* has births concentrated in March, indicating breeding activity some weeks earlier, perhaps in December, with gestation in the driest part of the year when sunshine for basking is most frequently available. Advent of the young is timed for a period of heavy precipitation. *M. brachypoda*, living in the drier climate of the Pacific versant, has its main breeding season delayed some four months later than that of *M. mabouya*. This results in a gestation that is timed for the early weeks of the rainy season, but in an area where there is generally sunshine for a part of each day permitting regular basking. Births are concentrated near the middle of the rainy season.

Basiliscus basiliscus has an annual schedule different from that of any other species and seemingly its populations differ notably among themselves at localities that are similar in habitat and not far apart. At Finca Taboga the dominant groups of young were from eggs probably laid in February, late March-April, July and August, with much less egg-laying at other times of year. At La Irma large crops of young resulted from egg-laying from October to November-December, and February. At Río Naranjo there were large broods from early November and December laying. On the Meseta Central there were broods from eggs laid in early December both at Turrúcares and Ojo de Agua.

A group of small to medium-sized, insectivorous species that are much alike in their annual cycles all occur in the Caribbean versant in climates of high rainfall and no marked dry season. They include *Basiliscus vittatus*, perhaps *B. plumifrons*, *Anolis limifrons*, *A. humilis*, *Scincella cherriei*, *Ameiva festiva*, *A. quadrilineata* and *Lepidoblepharis xanthostigma*. In all there is probably some breeding throughout the year. In *A. humilis* at Beverly there was relatively little egg production in January-March as compared with the rest of the year. In *A. limifrons* at Beverly

the same slowing in winter and spring was evident and it extended through April, with peak production in August and September. In *Basiliscus vittatus* at Portéte there was a three-month pause in reproduction that extended over much of November and to early February. In *Scincella cherriei* at Turrialba reproduction virtually stopped during a similar period—December to March. In these species reduced reproduction corresponds with the colder part of the year. However, the seasonal temperature change is slight, and each of the species lives and reproduces in cooler climates than those at the study areas. Seasonal variation in rainfall is much greater. February and March are usually by far the driest months of the year, with January and April also below average. Rainfall seems the most obvious variable that might affect level of reproductive activity. However, in *S. cherriei* and especially in *B. vittatus* the pause in breeding begins at a time when rainfall is still extremely high in November and December, hence it is not a direct result of reduced precipitation.

In a climate having little seasonal change in precipitation or temperature, it might be expected that population structure and level of reproductive activity would change but little in the course of an annual cycle. The species that was found most stable in this respect was *Anolis tropidolepis* at Hacienda El Prado on the Continental Divide in a cool moist climate. Although the amount of precipitation is much less in February, March and April than at other times of year, fog and rain are frequent at all seasons so moisture is never in short supply. Females of *A. tropidolepis* seem to produce eggs uninterruptedly throughout the year. Hatchlings and young of all sizes are always present and their ratios do not show any consistent trend; it is doubtful whether there is any significant seasonal change in the level of reproductive activity. *A. lionotus* also seems to reproduce throughout the year with no seasonal change at San Miguel de Sarapiquí. However, samples are relatively small for this species and are not ideally distributed through the year. Until more is known about the method of obtaining food and the sites of egg-laying, little can be said about the effect of precipitation on *A. lionotus*. In its streamside habitat moisture is never in short supply. Precipitation raises the stream level submerging rocks and logs that are used for perches at other times and reducing the open area at the edge of the water, in which most activity occurs. It reduces water temperature but increases the volume and rate of flow. It increases the quantity of floating arthropods, and probably decreases the availability of subaquatic arthropods, which are more dispersed and more deeply submerged.

LITERATURE CITED

Alvarez del Toro, M. 1960. Reptiles de Chiapas. Inst. Zool. del Estado Tuxtla Gutiérrez, Chiapas. 204 pp.

Ballinger, R. E., K. R. Marion, and O. J. Sexton. 1971. Thermal ecology of the lizard, *Anolis limifrons*, with comparative notes on three additional Panamanian anoles. Ecology 51: 246-254.

Bogert, C. M. 1949. Thermoregulation in reptiles, a factor in evolution. Evolution 3:195-211.

Bostic, D. L. 1966. A preliminary report of reproduction in the teiid lizard, *Cnemidophorus hyperythrus beldingi*. Herpetologica 22:81-90.

Brattstrom, B. H. 1965. Reptile body temperatures. Am. Midland Nat. 73:376-422.

Brooks, C. R. Jr. 1967. Population ecology of the ground skink, *Lygosoma laterale* (Say). Ecol. Monogr. 37:71-87.

Brown, E. E. 1956. Nests and young of the six-lined racerunner *Cnemidophorus sexlineatus* Linnaeus. J. Elisha Mitchell Sci. Soc. 72:30-40.

Campbell, H. W. 1971. Observations on the thermal activity of some tropical lizards of the genus *Anolis* (Iguanidae). Carib. J. Sci. 11: 17-20.

Carpenter, C. C. 1960. Reproduction in Oklahoma *Sceloporus* and *Cnemidophorus*. Herpetologica 16:175-182.

Davis, W. B., and J. R. Dixon. 1961. Reptiles (exclusive of snakes) of the Chilpancingo region, Mexico. Proc. Biol. Soc. Washington 74:37-56.

EVANS, L. T. 1951. Field study of the social behavior of the black lizard, *Ctenosaura pectinata*. Amer. Mus. Novit. No. 1493:1-26.

FITCH, H. S. 1956. Temperature responses of amphibians and reptiles in northeastern Kansas. Univ. Kansas Publ. Mus. Nat. Hist. 8:417-476.

———. 1958a. Natural history of the six-lined racerunner (*Cnemidophorus sexlineatus*). Univ. Kansas Publ. Mus. Nat. Hist. 11:11-62.

———. 1958b. Home ranges, territories and seasonal movements in vertebrates of the Reservation. Univ. Kansas Publ. Mus. Nat. Hist. 11:63-326.

———. 1968. Temperature and behavior of some equatorial lizards. Herpetologica 24:35-38.

———. 1970. Reproductive cycles of lizards and snakes. Univ. Kansas Mus. Nat. Hist. Misc. Publ. No. 52, pp. 1-247.

———. 1972. Ecology of *Anolis tropidolepis* in Costa Rican cloud forest. Herpetologica 28:10-21.

GREENE, H. W. 1969. Reproduction in a Middle American skink, *Leiolopisma cherriei* (Cope). Herpetologica 25:55-56.

HIRTH, H. F., 1963a. The ecology of two lizards on a tropical beach. Ecol. Monogr. 33:83-112.

———. 1963b. Some aspects of the natural history of *Iguana iguana* on a tropical strand. Ecology 44:613-619.

JENNSEN, T. A. 1970. The ethoecology of *Anolis nebulosus* (Sauria, Iguanidae). J. Herp. 4:1-38.

MARION, K. R., AND O. J. SEXTON. 1971. The reproductive cycle of the lizard *Sceloporus malachiticus* in Costa Rica. Copeia 1971:517-526.

MONTANUCCI, R. R. 1968. Comparative dentition in four iguanid lizards. Herptologica 24:305-315.

NEILL, W. T., AND R. ALLEN. 1959. Studies on the amphibians and reptiles of British Honduras. Publ. Res. Div. Ross Allen's Rept. Inst. 2:1-76.

ORTLEB, E. P. 1965. Hatching of basilisk eggs. Herpetologica 20:277-279.

PETERS, J. A., AND R. DONOSO-BARROS. 1970. Catalog of the Neotropical Squamata: Part II. Lizards and Amphisbaenians. Smithsonian Inst. U.S. Nat. Mus. Bull. 297. 293 pp.

QUESNEL, V. C. 1957. The life history of the streak gecko *Gonatodes vittatus* (Licht.). J. Trinidad Field Nat. Club 1957:5-14.

RAND, A. S. 1968. A nesting aggregation of iguanas. Copeia 1968:552-561.

RUIBAL, R. 1961. Thermal relations of five species of tropical lizards. Evolution 15:98-111.

SCHOENER, T. 1968. The *Anolis* lizards of Bimini: resources partitioning in a complex fauna. Ecology 49:704-726.

SCOTT, N. J. 1966. Ecologically important aspects of the climates of Costa Rica. (Mimeographed syllabus, Organization for Tropical Studies, February-March 1966.)

SERVICIO METEOROLÓGICO NACIONAL. 1966, 1967, 1968. Anuario Meteorológico, San José (annual mimeographed summaries of weather data).

SEXTON, O. J., E. P. ORTLEB, L. M. HATHAWAY, R. E. BALLINGER AND P. LICHT. 1971. Reproductive cycles of three species of anoline lizards from the Isthmus of Panama. Ecology 52:201-215.

SEXTON, O. J., AND O. TURNER. 1971. The reproductive cycle of a neotropical lizard. Ecology 52:159-164.

SMITH, R. E. 1968. Studies on reproduction in Costa Rican *Ameiva festiva* and *Ameiva quadrilineata* (Sauria, Teiidae). Copeia 1968: 236-239.

STEBBINS, R. C., AND H. B. ROBINSON. 1946. Further analysis of a population of the lizard, *Sceloporus graciosus gracilis*. Univ. California Publ. Zool. 48:148-168.

TAYLOR, E. H. 1956. A review of the lizards of Costa Rica. Univ. Kansas Sci. Bull. 38 Pt. 1: 1-322.

TURNER, F. B., R. I. JENNRICH AND J. D. WEINTRAUB. 1969. Home ranges and body size of lizards. Ecology 50:1076-1081.

WEBB, R. G. 1958. The status of the Mexican lizards of the genus *Mabuya*. Univ. Kansas Sci. Bull. 38 Pt. II:1303-1313.

WILLIAMS, K. L., AND H. M. SMITH. 1966. Noteworthy lizards of the genus *Anolis* from Costa Rica. Carib. J. Sci. 6:163-166.

EXPLANATION OF PLATES

Plate I. **Upper,** fence in San José utilizing yuccas and other trees as posts; **lower,** study area no. 2 at Playas del Coco; many *Sceloporus variabilis* lived on spiny trunks of the two large trees *(Bombacopsis quinata).*

PLATE II. **Upper,** beach wrack at Boca de Barranca; **middle,** upper beach at Boca de Barranca; **lower,** log jam in the dry season at Río Congo, La Irma.

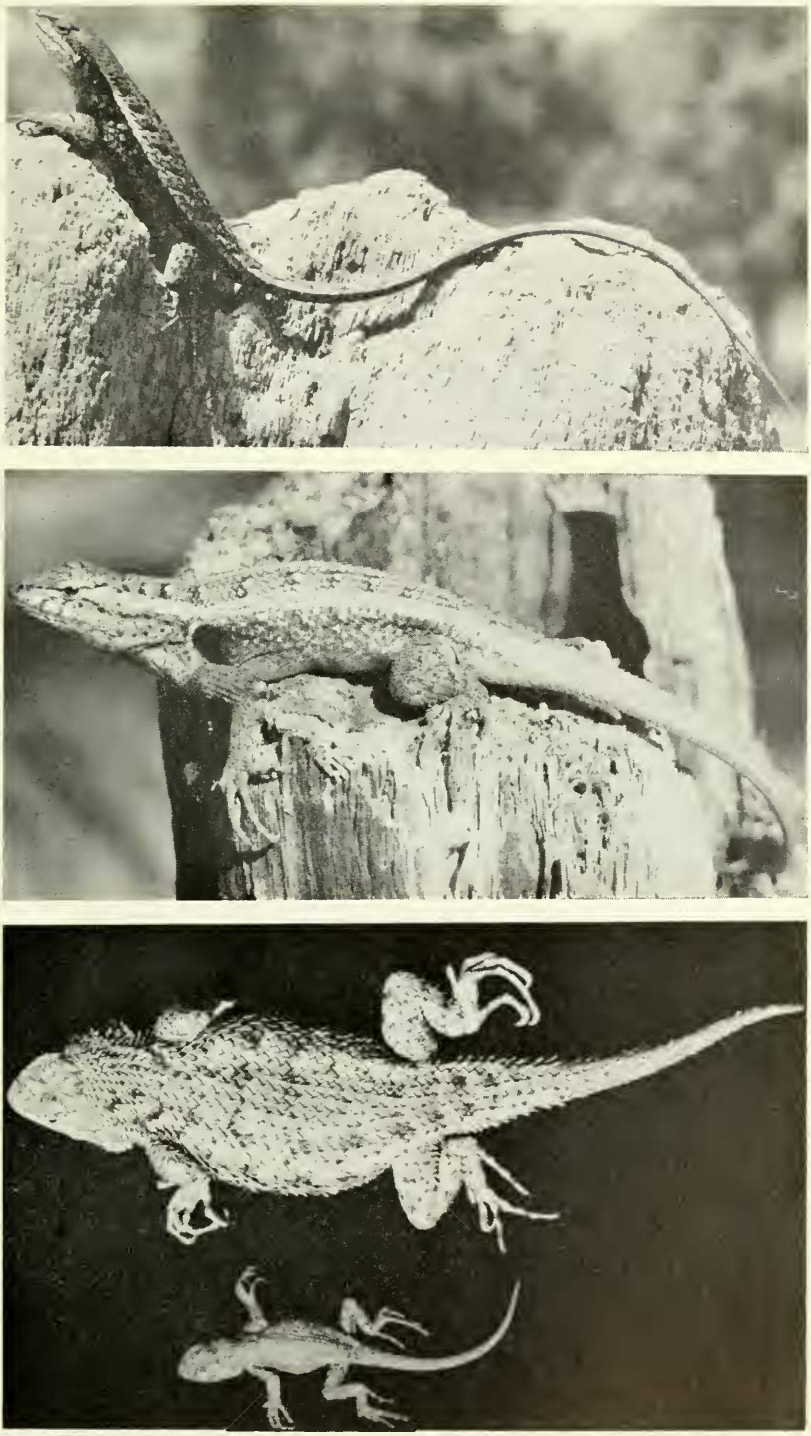

Plate III. **Upper,** *Sceloporus squamosus,* adult male, Playas del Coco; **middle,** *Sceloporus variabilis,* adult male, Playas del Coco; **lower,** *Scelophorus malachiticus,* adult female with one of her five newborn young, Hacienda El Prado.

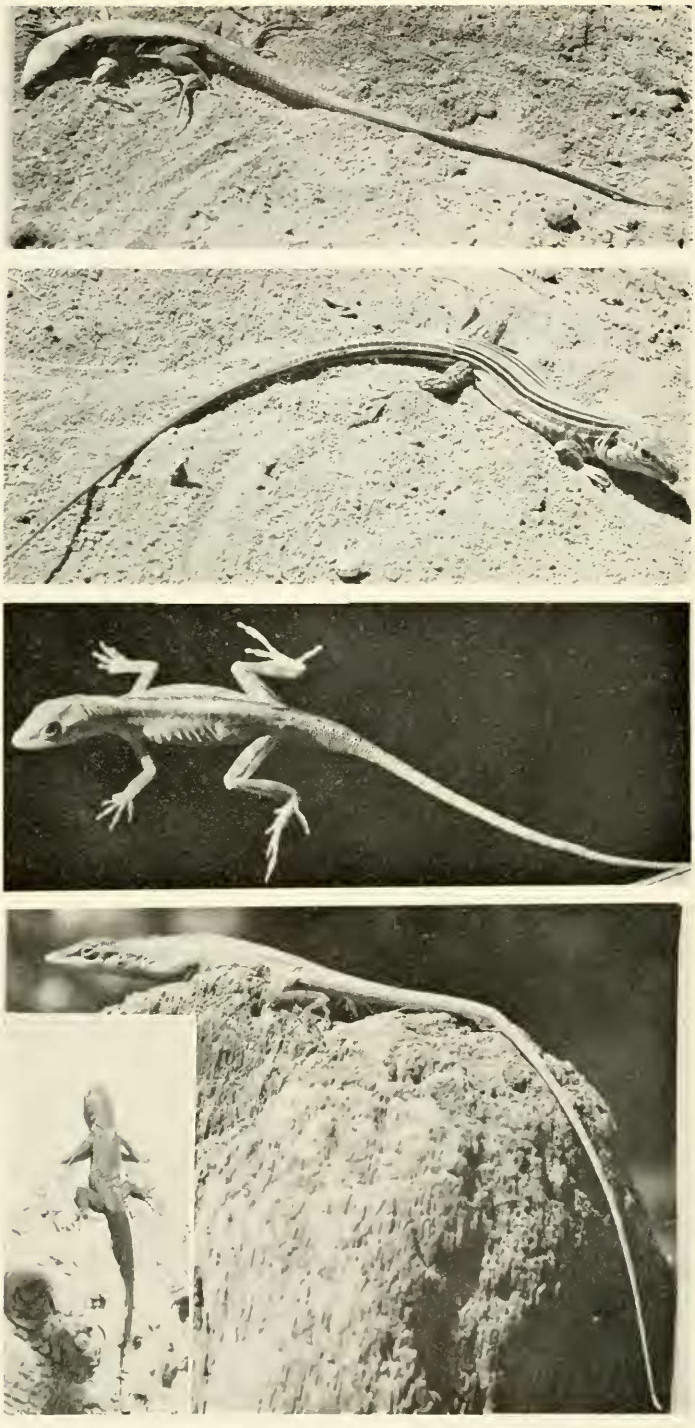

PLATE IV. **Upper,** *Ameiva undulata,* adult male, Sardinal; **upper middle,** *Cnemidophorus deppii,* adult male, Boca de Barranca; **lower middle,** *Anolis cupreus,* adult male, San José; **lower,** *Anolis sericeus,* adult male, La Irma; **lower left,** *Gonatodes albogularis,* adult male, Boca de Barranca.